Robustness of optimal intermittent search strategies in dimension 1, 2 and 3

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Abstract

Search problems at various scales involve a searcher, be it a molecule before reaction or a foraging animal, which performs an intermittent motion. Here we analyze a generic model based on such type of intermittent motion, in which the searcher alternates phases of slow motion allowing detection, and phases of fast motion without detection. We present full and systematic results for different modeling hypotheses of the detection mechanism in space dimension 1, 2 and 3. Our study completes and extends the results of our recent letter [Loverdo *et al.* Nature Physics **4**, 134 (2008)] and gives the necessary calculation details. In addition, a new modeling of the detection phase is presented. We show that the mean target detection time can be minimized as a function of the mean duration of each phase in dimension 1, 2 and 3. Importantly, this optimal strategy does not depend on the details of the modeling of the slow detection phase, which shows the robustness of our results. We believe that this systematic analysis can be used as a basis to study quantitatively various real search problems involving intermittent behaviors.

PACS numbers:

I. INTRODUCTION

Search problems, involving a "searcher" and a "target", pop up in a wide range of domains. They have been subject of intense work of modeling in situations as various as castaway rescue [1], foraging animals [2, 3, 4, 5, 6, 7, 8, 9] or proteins reacting on a specific DNA sequence [10, 11, 12, 13, 14, 15, 16, 17, 18, 19]. Among the wide panel of search strategies, the so-called intermittent strategies – combining "slow" phases enabling detection of the targets and "rapid" phases during which the searcher is unable to detect the targets – have been proved to be relevant at various scales.

Indeed, at the macroscopic scale, numerous animal species have been reported to perform such kind of intermittent motion [20, 21] while searching either for food, shelter or mate. In the case of an exploratory behavior, i.e. when the searcher has no previous knowledge or "mental map" of the location of targets, trajectories can be considered as random. Actually, the observed search trajectories are often described as a sequence of ballistic segments interrupted by much slower phases. These slow, and sometimes even immobile [21], phases are not always well characterized, but it seems clear that they are aimed at sensing the environment and trying to detect the targets [22]. On the other hand, during the fast moving phases, perception is generally degraded so that the detection is very unlikely. An example of such intermittent behavior is given by the *C.elegans* worm, which alternates between a fast and almost straight displacement ("roaming") and a much more sinuous and slower trajectory ("dwelling") [23]. During this last phase, the worm's head, bearing most of its sensory organs, moves and touches the surface nearby.

Intermittent strategies are actually also relevant at the microscopic scale, as exemplified by reaction kinetics in biological cells [10, 24]. As the cellular environment is intrinsically out of equilibrium, the transport of a given tracer particle which has to react with a target molecule cannot be described as mere thermal diffusion : if the tracer particle can indeed diffuse freely in the medium, it also intermittently binds and unbinds to motor proteins, which perform an active ballistic motion powered by ATP hydrolysis along cytoskeletal filaments [24, 25, 26]. Such intermittent trajectories of reactive particles are observed for example in the case of vesicles before they react with their target membrane proteins [26]. In that case, targets are not accessible during the ballistic phases when the vesicle is bound to motors, but only during the free diffusive phase.

As illustrated in the previous examples the search time is often a limiting quantity whose optimization can be very beneficial for the system – be it an animal or a single cell. In the case of intermittent search strategies, the minimization of the search time can be qualitatively discussed : on the one hand, the fast but non-reactive phases can appear as a waste of time, since they do not give any chance of target detection. On the other hand, such fast phases can provide an efficient way to relocate and explore space. This puts forward the following questions : is it beneficial for the search to perform such fast but non reactive phases? Is it possible, by properly tuning the kinetic parameters of trajectories (such as the durations of each of the two phases) to minimize the search time? These questions have been addressed quantitatively on specific examples in [6, 7, 8, 9, 24, 27, 28, 29, 30], where it was shown that intermittent search strategies can be optimized. In this paper, we perform a systematic analytical study of intermittent search strategies in dimensions 1,2 and 3 and fully characterize the optimal regimes. This study completes our previous works, and in particular our recent letter [24], by providing all calculations details and specifying the validity domains of our approach. It also presents new cases of potential relevance to model real search problems. Overall, this systematic approach allows us to identify robust features of intermittent search strategies. In particular, the slow phase that enables detection is often hard to characterize experimentally. Here we propose and study 3 distinct modelings for this phase, which allows us to assess to which extent our results are robust and model dependent. Our analysis covers in details intermittent search problems in dimension 1, 2 and 3, and is aimed at giving a quantitative basis – as complete as possible – to model real search problems involving intermittent searchers.

We first define our model and give general notations that we will use in this article. Then we systematically examine each case, studying the search problem in dimension 1, 2 and 3, where for each dimension different types of motion in the slow phase are considered. Each case is ended by a short summary, and we highlight the main results for each dimension. Eventually we synthesize the results in the table II where all cases, their differences and similarities are gathered. This table finally leads us to draw general conclusions.

II. MODEL AND NOTATIONS

A. Model

The general framework of the model relies on intermittent trajectories, which have been put forward for example in [6]. We consider a searcher that switches between two phases. The switching rate λ_1 (resp. λ_2) from phase 1 to phase 2 (resp. from phase 2 to phase 1) is time-independent, which assumes that the searcher has no memory and implies an exponential distribution of durations of each phase i of mean $\tau_i = 1/\lambda_i$.

Phase 1 denotes the phase of slow motion, during which the target can be detected if it lies within a distance from the searcher which is smaller than a given detection radius a. a is the maximum distance within which the searcher can get information about target location. We propose 3 different modelings of this phase, in order to cover various real life situations.

- In the first modeling of phase 1, hereafter referred to as the "static mode", the searcher is immobile, and detects the target with probability per unit time k if it lies at a distance less than a.
- In the second modeling, called the "diffusive mode", the searcher performs a continuous diffusive motion, with diffusion coefficient D, and finds immediately the target if it lies at a distance less than a.
- In the last modeling, called the "ballistic mode", the searcher moves ballistically in a random direction with constant speed v_l and reacts immediately with the target if it lies at a distance less than a.

Some comments on these different modelings of the slow phase 1 are to be made. The first two modes have already been introduced [8, 24], while the analysis of the ballistic mode has never been performed. These 3 modes schematically cover experimental observations of the behavior of animals searching for food [20, 21], where the slow phases of detection are often described as either static, random or with slow velocity. Several real situations are likely to involve a combination of two modes. For instance the motion of a reactive particle in a cell not bound to motors can be described by a combination of the diffusive and static modes. For the sake of simplicity, here we treat these modes independently, and our approach can therefore be considered as a limit of more realistic models. We note that a similar

version of the ballistic mode of detection has been discussed by Viswanathan et al.[2, 31]. They introduced a model searcher performing randomly oriented ballistic movements (and of power law distributed duration), with detection capability all along the trajectory. For this 1 state searcher, the search time for a target (which is assumed to disappear after the first encounter) is minimized when the searcher performs a purely ballistic motion and never reorientates. In fact, the ballistic mode version of our model extends this model of 1 state ballistic searcher, by allowing the searcher to switch to a mode of faster motion, but with no perception. As it will be discussed, adding this possibility of intermittence enables a further minimization of the search time. Finally, combining these three schematic modes covers a wide range of possible motions, from subdiffusive (even static), diffusive, to superdiffusive (even ballistic).

The phase 2 denotes the fast phase during which the target cannot be found. In this phase, the searcher performs a ballistic motion at constant speed V and random direction, redrawn each time the searcher enters a phase 2, independently of previous phases. In real examples correlations between successive phases could exist. If correlations are very high, it is close to a 1-dimensional problem with all the phases 2 in the same direction, a different problem already treated in [6]. We consider here the limit of low correlation, that is of a searcher with no memory skills.

We assume that the searcher evolves in d-dimensional spherical domain of radius b, with reflective boundaries and with one centered immobile target (bounds can be obtained in the case of mobile targets [32, 33]). As the searcher does not initially know the target location, we start the walk from a random point of the d-dimensional sphere, and average the mean target detection time over the initial position. This geometry models the case of a single target in a finite domain, and also provides a good approximation of an infinite space with regularly spaced targets. Such regular array of targets corresponds to a mean-field approximation of random distributions of targets, which can be more realistic in some experimental situations. We note that in the 1 dimensional case, we have shown that a Poisson distribution of targets can lead to significantly different results from the regular distribution[34, 35]. We expect this difference to be less in dimension 2 and 3, and we limit ourselves in this paper to the mean field treatment for the sake of simplicity.

B. Notations

$t_i(\vec{r})$ denotes the mean first passage time on the target, for a searcher *starting* in the phase i from point $\vec{r}$, where phase $i = 1$ is the slow motion phase with detection and phase $i = 2$ is the fast motion phase without target detection. Note that in dimension 1, the space coordinate will be denoted by x, and in the case of a ballistic mode for phase 1, the upper index in $t_i^{\pm}$ stands for ballistic motion with direction $\pm x$. The general method which will be used at length in this paper, consists in deriving and solving backward equations for $t_i(\vec{r})$ [36]. These linear equations involve derivatives with respect to the starting position $\vec{r}$.

Assuming that the searcher starts in phase 1, the mean detection time for a target is then defined as :

$$t_m = \frac{1}{V(\Omega_d)} \int_{\Omega_d} t_1(\vec{r}) d\vec{r} \tag{1}$$

with Ω_d the d-dimensional sphere of radius b and $V(\Omega_d)$ its volume. Unless specified, we will consider the low target density limit $a \ll b$.

Our general aim is to minimize t_m as a function of the mean durations τ_1, τ_2 of each phase, and in particular to determine under which conditions an intermittent strategy (with finite τ_2) is faster than a usual 1 state search in the phase 1 only, which is given by the limit $\tau_1 \to \infty$. In the static mode, intermittence is necessary for the searcher to move, and is therefore always favorable. In the diffusive mode, we will compare the mean search time with intermittence t_m to the mean search time for a 1 state diffusive searcher t_{diff}, and define the gain as $gain = t_{diff}/t_m$. Similarly in the ballistic mode, we will compare t_m to the mean search time for a 1 state ballistic searcher t_{bal} and define the gain as $gain = t_{bal}/t_m$.

Throughout the paper, the upper index "opt" is used to denote the value of a parameter or variable at the minimum of t_m .

III. DIMENSION 1

Besides the fact that it involves more tractable calculations, the 1-dimensional case can also be interesting to model real search problems. At the microscopic scale, tubular structures of cells such as axons or dendrites in neurons can be considered as 1-dimensional [25]. The active transport of reactive particles, which alternate diffusion phases and ballistic phases when bound to molecular motors, can be schematically captured by our model with

diffusive mode [24]. At the macroscopic scale, one could cite animals like ants [37] which tend to follow tracks or one-dimensional boundaries.

A. Static mode

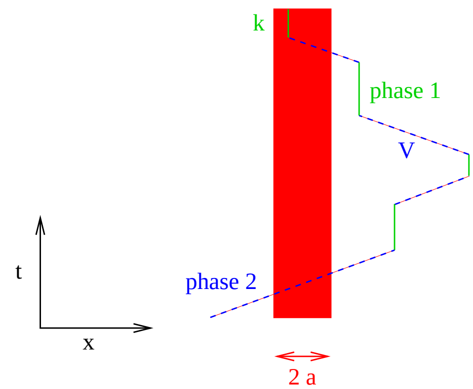

Figure 1: (Color online) Static mode in dimension 1

In this section we assume that the detection phase is modeled by the static mode. Hence the searcher does not move during the reactive phase 1, and has a fixed reaction rate k per unit time with the target if it lies within its detection radius a. It is the limit of a very slow searcher in the reactive phase.

1. Equations

Outside the target (for $x > a$, we have the following backward equations for the mean first-passage time :

$$V\frac{dt_2^+}{dx} + \frac{1}{\tau_2}(t_1 - t_2^+) = -1 \tag{2}$$

$$-V\frac{dt_2^-}{dx} + \frac{1}{\tau_2}(t_1 - t_2^-) = -1 \tag{3}$$

$$\frac{1}{\tau_1}\left(\frac{t_2^+ + t_2^-}{2} - t_1\right) = -1 \tag{4}$$

Inside the target ($x \le a$), the first two equations are identical, but the third one is written :

$$\frac{1}{\tau_1}\frac{t_2^+ + t_2^-}{2} - \left(\frac{1}{\tau_1} + k\right)t_1 = -1. \tag{5}$$

We introduce $t_2 = \frac{t_2^+ + t_2^-}{2}$ and $t_2^d = \frac{t_2^+ - t_2^-}{2}$. Then outside the target we have the following equations :

$$V\frac{dt_2}{dx} - \frac{1}{\tau_2}t_2^d = 0 \tag{6}$$

$$V^2\tau_2\frac{d^2t_2}{dx^2} + \frac{1}{\tau_2}(t_1 - t_2) = 0 \tag{7}$$

$$\frac{1}{\tau_1}(t_2 - t_1) = -1. \tag{8}$$

Inside the target the first two equations are identical, but the last one writes :

$$\frac{1}{\tau_1}t_2 - \left(\frac{1}{\tau_1} + k\right)t_1 = -1. \tag{9}$$

Due to the symmetry $x \leftrightarrow -x$, we can restrict the study to the part $x \in [0, a]$ and the part $x \in [a, b]$. This symmetry also implies :

$$\left.\frac{dt_2^{in}}{dx}\right|_{x=0} = 0 \tag{10}$$

$$\left.\frac{dt_2^{out}}{dx}\right|_{x=b} = 0. \tag{11}$$

In addition, continuity at $x = a$ for t_2^+ and t_2^- gives:

$$t_2^{in}(x = a) = t_2^{out}(x = a) \tag{12}$$

$$t_2^{d,in}(x = a) = t_2^{d,out}(x = a). \tag{13}$$

This set of linear equations enables an explicit determination of t_1, t_2, t_2^d inside and outside the target.

2. *Results*

An exact analytical expression of the mean first passage time at the target is then given by :

$$t_m = \frac{\tau_1 + \tau_2}{b}\left(\frac{b}{k\tau_1} + \frac{(b-a)^3}{3V^2\tau_2^2} + \frac{\beta(b-a)^2}{V\tau_2}coth\left(\frac{a}{V\tau_2\beta}\right) + (b-a)\beta^2\right) \tag{14}$$

where $\beta = \sqrt{(k\tau_1)^{-1} + 1}$.

In order to determine the optimal strategy, we need to simplify this expression, by expanding (14) in the regime $b \gg a$:

$$t_m = (\tau_1 + \tau_2)\left(\frac{1}{k\tau_1} + \frac{b^2}{3V^2\tau_2^2} + \frac{\beta b}{V\tau_2}coth\left(\frac{a}{V\tau_2\beta}\right) + \beta^2\right) \tag{15}$$

We make the further assumption $\frac{a}{V\tau_2} \ll 1$ and obtain, using $\beta > 1$:

$$t_m = (\tau_1 + \tau_2)\left(\frac{1}{k\tau_1} + \frac{b^2}{3V^2\tau_2^2} + \beta^2\frac{b}{a} + \beta^2\right) \tag{16}$$

Since $\beta > 1$ and $\beta > 1/(k\tau_1)$, we obtain in the limit $b \gg a$:

$$t_m = (\tau_1 + \tau_2)\left(\frac{b^2}{3V^2\tau_2^2} + \left(\frac{1}{k\tau_1} + 1\right)\frac{b}{a}\right) \tag{17}$$

This simple expression gives a very good and convinient approximation of the mean first passage time at the target as shown in Fig.2.

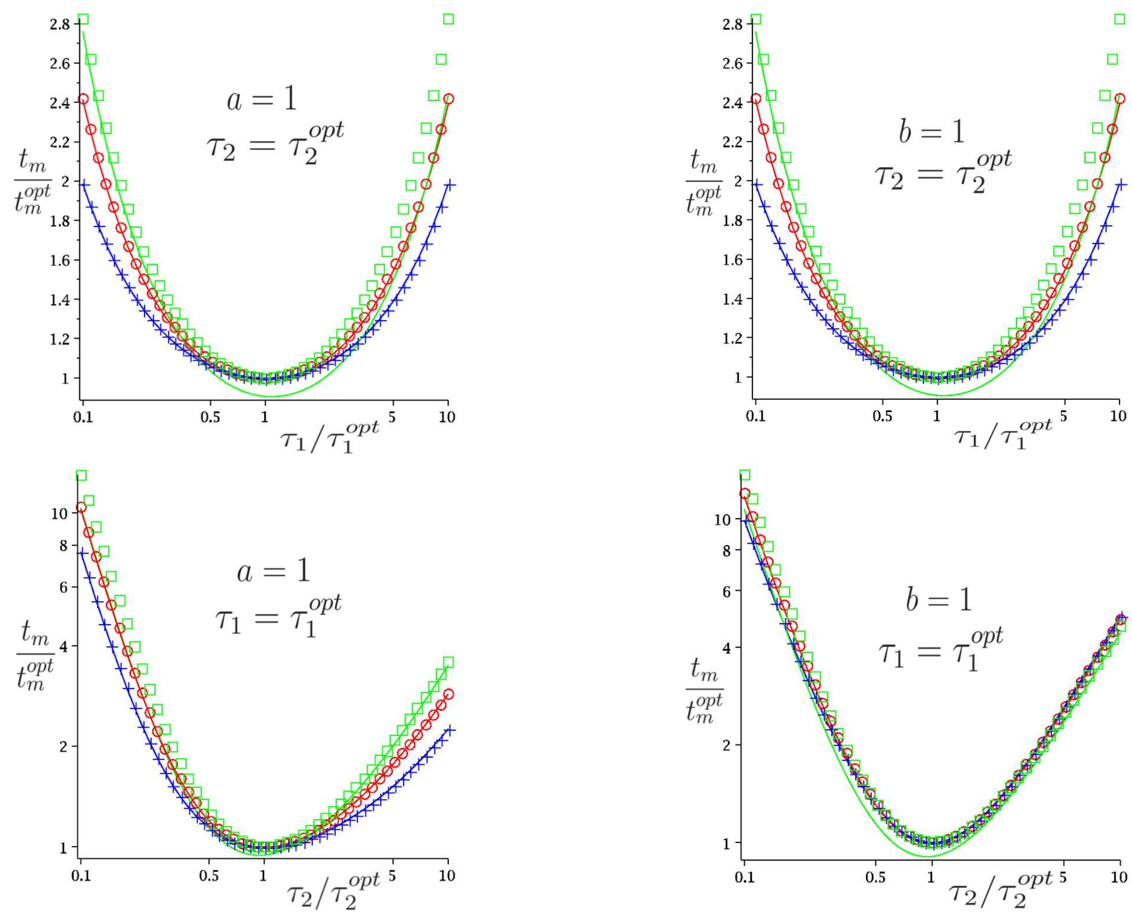

Figure 2: (Color online) Static mode in 1 dimension. Exact expression of t_m (14) (lines) compared to the approximation of t_m (17) (symbols), both rescaled by t_m^{opt} (20). τ_1^{opt} from (18), τ_2^{opt} from (19). $V = 1$, $k = 1$. $b/a = 10$ (green, squares), $b/a = 100$ (red, circles), $b/a = 1000$ (blue, crosses).

We use this approximation (17) to find τ_1 and τ_2 values which minimize t_m :

$$\tau_1^{opt} = \sqrt{\frac{a}{Vk}}\left(\frac{b}{12a}\right)^{1/4} \tag{18}$$

$$\tau_2^{opt} = \frac{a}{V}\sqrt{\frac{b}{3a}}. \tag{19}$$

It can be noticed than τ_2^{opt} does not depend on k. Then the expression of the minimal value of the search time t_m (17) with $\tau_1 = \tau_1^{opt}$ and $\tau_2 = \tau_2^{opt}$ is :

$$t_m^{opt} = \frac{b}{ak}\left(\frac{b}{3a}\right)^{1/4}\left(\sqrt{\frac{2bk}{3V}}\left(\frac{3a}{b}\right)^{1/4} + 1\right)\left(\sqrt{\frac{2ka}{V}} + \left(\frac{3a}{b}\right)^{1/4}\right). \tag{20}$$

3. Summary

For the static modeling of the detection phase in dimension 1, in the $b \gg a$ limit, the mean detection time is :

$$t_m = (\tau_1 + \tau_2)\left(\frac{b^2}{3V^2\tau_2^2} + \left(\frac{1}{k\tau_1} + 1\right)\frac{b}{a}\right). \tag{21}$$

Intermittence is always favorable, and the optimal strategy is realized when $\tau_1^{opt} = \sqrt{\frac{a}{Vk}}\left(\frac{b}{12a}\right)^{1/4}$ and $\tau_2^{opt} = \frac{a}{V}\sqrt{\frac{b}{3a}}$. Importantly, the optimal duration of the relocation phase does not depend on k, i.e. on the description of the detection phase.

B. Diffusive mode

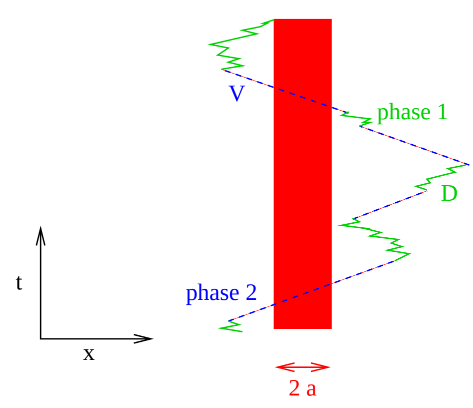

Figure 3: (Color online) Diffusive mode in one dimension

We now turn to the diffusive modeling of the detection phase. The detection phase 1 is now diffusive, with immediate detection of the target if it is within a radius a from the searcher.

1. Equations

Along the same lines, the backward equations for the mean first-passage time read outside the target $(x > a)$:

$$V\frac{dt_2^+}{dx} + \frac{1}{\tau_2}(t_1 - t_2^+) = -1 \tag{22}$$

$$-V\frac{dt_2^-}{dx} + \frac{1}{\tau_2}(t_1 - t_2^-) = -1 \tag{23}$$

$$D\frac{d^2t_1}{dx^2} + \frac{1}{\tau_1}\left(\frac{t_2^+}{2} + \frac{t_2^-}{2} - t_1\right) = -1, \tag{24}$$

and inside the target $(x \leq a)$:

$$V\frac{dt_2^+}{dx} - \frac{1}{\tau_2}t_2^+ = -1 \tag{25}$$

$$-V\frac{dt_2^-}{dx} - \frac{1}{\tau_2}t_2^- = -1 \tag{26}$$

$$t_1 = 0. \tag{27}$$

We introduce the variables $t_2 = \frac{t_2^+ + t_2^-}{2}$ and $t_2^d = \frac{t_2^+ - t_2^-}{2}$. This leads to the following system outside the target $(x > a)$:

$$V\frac{dt_2}{dx} = \frac{1}{\tau_2}t_2^d \tag{28}$$

$$V^2\tau_2\frac{dt_2}{dx} + \frac{1}{\tau_2}(t_1 - t_2) = -1 \tag{29}$$

$$D\frac{d^2t_1}{dx^2} + \frac{1}{\tau_1}(t_2 - t_1) = -1, \tag{30}$$

and inside the target $(x \leq a)$:

$$V\frac{dt_{2,in}}{dx} = \frac{1}{\tau_2}t_{2,in}^d \tag{31}$$

$$V^2\tau_2\frac{dt_{2,in}}{dx} - \frac{1}{\tau_2}t_{2,in} = -1 \tag{32}$$

$$t_1 = 0. \tag{33}$$

Interestingly, this system is exactly of the same type that what would be obtained with 2 diffusive phases, with $D_2^{eff} = V^2\tau_2$ in phase 2. Boundary conditions result from continuity and symmetry :

$$t_1(a) = 0 \tag{34}$$

$$t_2^+(a) = t_{2,in}^+(a) \tag{35}$$

$$t_2^-(a) = t_{2,in}^-(a) \tag{36}$$

$$\left.\frac{dt_2}{dx}\right|_{x=b} = 0 \tag{37}$$

$$\left.\frac{dt_1}{dx}\right|_{x=b} = 0 \tag{38}$$

$$\left.\frac{dt_{2,in}}{dx}\right|_{x=0} = 0. \tag{39}$$

2. Results

Standard but lengthy calculations lead to an exact expression of mean first detection time of the target t_m given in appendix VII A 1. We first studied numerically the minimum of t_m in appendix VII A 2, and identified 3 regimes. In the first regime ($b < \frac{D}{V}$) intermittence is not favorable. For $b > \frac{D}{V}$ intermittence is favorable and two regimes ($\frac{bD^2}{a^3V^2} < 1$ and $\frac{bD^2}{a^3V^2} > 1$) should be distinguished . We now study analytically each of these regimes.

3. Regime where intermittence is not favorable : $b < \frac{D}{V}$

If $b < \frac{D}{V}$, the time spent to explore the search space is smaller in the diffusive phase than in the ballistic phase. Intermittence cannot be favorable in this regime, as confirmed by the numerical study in appendix VII A 2.

Without intermittence, the searcher only performs diffusive motion and the problem can be solved straightforwardly. The backward equations read $t_{diff} = 0$ inside the target ($x \leq a$), and outside the target ($x > a$) :

$$D\frac{d^2 t_{diff}}{dx^2} = -1. \tag{40}$$

Since $t_{diff}(x = a) = 0$ and $\left.\frac{dt_{diff}}{dx}\right|_{x=b} = 0$, we get $t_{diff}(x) = \frac{1}{2D}((b-a)^2 - (b-x)^2)$. The mean first passage time at the target then reads :

$$t_{diff} = \frac{(b-a)^3}{3Db}, \tag{41}$$

which in the limit $b \gg a$ leads to :

$$t_{diff} \simeq \frac{b^2}{3D}. \tag{42}$$

4. *Optimization in the first regime where intermittence is favorable : $b < \frac{D}{V}$ and $\frac{bD^2}{a^3V^2} \gg 1$*

As explained in details in appendix VII A 3, we use the approximation of low target density ($b \gg a$), and we use assumptions on the dependence of τ_1^{opt} and τ_2^{opt} on b and a. These assumptions lead to the following approximation of the mean first passage time :

$$t_m = (\tau_1 + \tau_2)\, b \left(\frac{b}{3V^2\tau_2^2} + \frac{1}{\sqrt{D\tau_1}} \right). \tag{43}$$

We checked numerically that this expression gives a good approximation of t_m in this regime, in particular around the optimum (Fig.4).

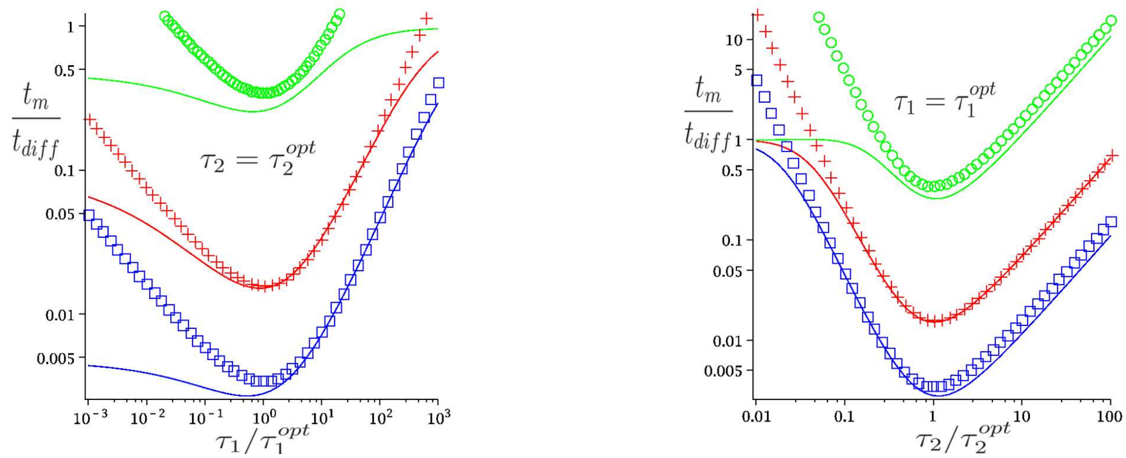

Figure 4: (Color online) Diffusive mode in 1 dimension. $\frac{t_m}{t_{diff}}$, t_{diff} from (42), and t_m exact expression (158) (line), approximation in the regime of favorable intermittence and $\frac{bD^2}{a^3V^2} \gg 1$ (43) (symbols). $a = 1$ and $b = 100$ (green, circles), $a = 1$, $b = 10^4$ (red, crosses), $a = 10$, $b = 10^5$ (blue, squares). $D = 1$, $V = 1$. τ_1^{opt} is from expression (44), τ_2^{opt} is from expression (45)

The simplified t_m expression (43) is minimized for :

$$\tau_1^{opt} = \frac{1}{2}\sqrt[3]{\frac{2b^2D}{9V^4}} \tag{44}$$

$$\tau_2^{opt} = \sqrt[3]{\frac{2b^2D}{9V^4}} \tag{45}$$

$$t_m^{opt} \simeq \sqrt[3]{\frac{3^5}{2^4}\frac{b^4}{DV^2}}. \tag{46}$$

This compares to the case without intermittence (41) according to :

$$gain^{opt} = \frac{t_{diff}}{t_m^{opt}} \simeq \sqrt[3]{\frac{2^4}{3^8}} \left(\frac{bV}{D}\right)^{\frac{2}{3}} \simeq 0.13 \left(\frac{bV}{D}\right)^{\frac{2}{3}}. \tag{47}$$

These results are in agreement with numerical minimization of the exact t_m (Table III in appendix VII A 2).

5. *Optimization in the second regime where intermittence is favorable : $b < \frac{D}{V}$ and $1 \gg \frac{bD^2}{a^3V^2}$*

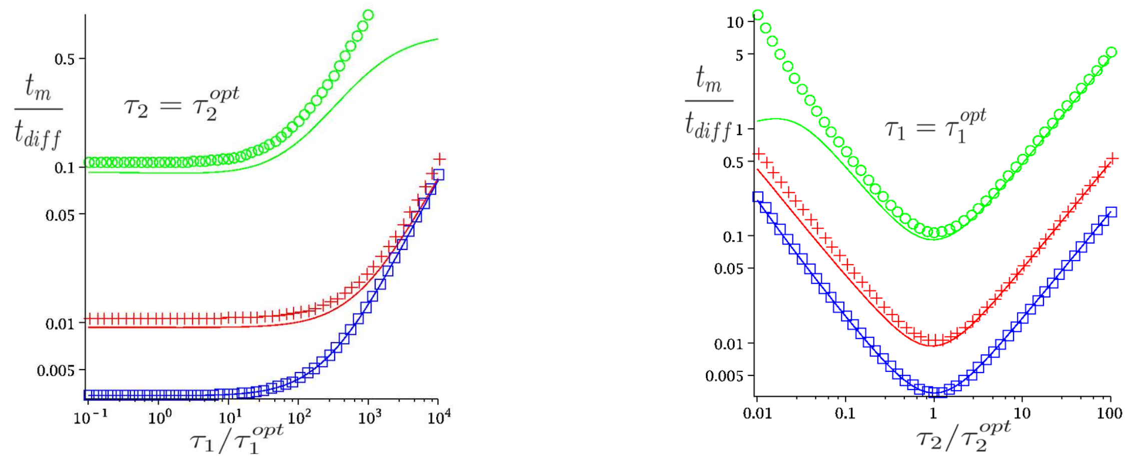

Figure 5: (Color online) Diffusive mode in 1 dimension. $\frac{t_m}{t_{diff}}$, t_{diff} from (42), and t_m exact expression (158) (line), approximation in the regime of favorable intermittence and $\frac{bD^2}{a^3V^2} \ll 1$ (48) (symbols). $a = 10$ and $b = 100$ (green, circles), $a = 10$, $b = 1000$ (red, crosses), $a = 100$, $b = 10^4$ (blue, squares). $D = 1$, $V = 1$. τ_1^{opt} is from expression (49), τ_2^{opt} is from expression (50)

We start from the exact expression of t_m (158). As detailed in appendix VII A 4, we make assumptions on the dependence of τ_1^{opt} and τ_2^{opt} with b and a, and use the assumptions that $b \gg a$ and $1 \gg \frac{bD^2}{a^3V^2}$. It leads to :

$$t_m \simeq \frac{b}{a}(\tau_1 + \tau_2)\left(\frac{a}{a + \sqrt{D\tau_1}} + \frac{ab}{3V^2\tau_2^2}\right). \tag{48}$$

This expression gives a good approximation of t_m, at least around the optimum (Fig.5), which is characterized by:

$$\tau_1^{opt} = \frac{Db}{48V^2a} \tag{49}$$

$$\tau_2^{opt} = \frac{a}{V}\sqrt{\frac{b}{3a}} \tag{50}$$

$$t_m^{opt} \simeq \frac{2a}{v\sqrt{3}}\left(\frac{b}{a}\right)^{3/2} \tag{51}$$

$$gain \simeq \frac{1}{2\sqrt{3}}\frac{aV}{D}\sqrt{\frac{b}{a}}. \tag{52}$$

These results are in very good agreement with numerical data (Table III in appendix VII A 2). Note that the gain can be very large at low target density.

6. Summary

We calculated explicitly the mean first passage time t_m in the case where the detection phase is modeled by the diffusive mode. We minimized t_m as a function of τ_1 and τ_2, the mean phases durations, with the assumption $a \ll b$. There are three regimes:

- when $b < \frac{D}{V}$, intermittence is not favorable. $\tau_1^{opt} \to \infty$, $\tau_2^{opt} \to 0$, $t_m^{opt} = t_{diff} \simeq \frac{b^2}{3D}$
- when $b > \frac{D}{V}$ and $\frac{bD^2}{a^3V^2} \gg 1$, intermittence is favorable, with $\tau_2^{opt} = 2\tau_1^{opt} = \sqrt[3]{\frac{2b^2D}{9V^4}}$, and $t_m^{opt} \simeq \sqrt[3]{\frac{3^5}{2^4}\frac{b^4}{DV^2}}$
- when $b > \frac{D}{V}$ and $\frac{bD^2}{a^3V^2} \ll 1$, intermittence is favorable, with $\tau_1^{opt} = \frac{Db}{48V^2a}$, $\tau_2^{opt} = \frac{a}{V}\sqrt{\frac{b}{3a}}$, $t_m^{opt} \simeq \frac{2a}{v\sqrt{3}}\left(\frac{b}{a}\right)^{3/2}$.

This last regime is of particular interest, since the value obtained for τ_2^{opt} is the same as in the static mode (cf. section III A 3).

C. Ballistic mode

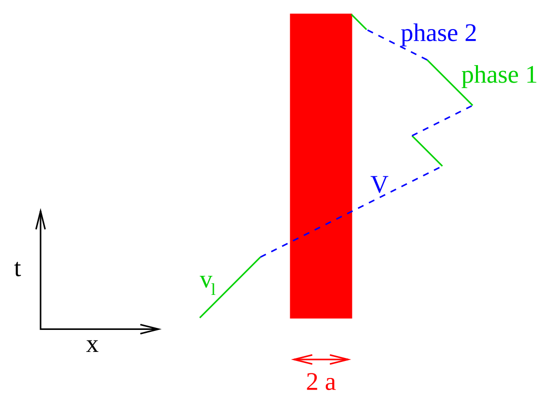

Figure 6: (Color online) Ballistic mode in one dimension

We now treat the case where the detection phase 1 is modeled by the ballistic mode. This model schematically accounts for the general observation that speed often degrades perception abilities. Our model corresponds to the extreme case where only two modes are available : either the motion is slow and the target can be found, or the motion is fast and the target cannot be found. Note that this model can be compared with [2].

1. Equations

The backward equations read outside the target $(x > a)$:

$$v_l \frac{dt_1^+}{dx} + \frac{1}{\tau_1}\left(\frac{t_2^+}{2} + \frac{t_2^-}{2} - t_1^+\right) = -1 \tag{53}$$

$$-v_l \frac{dt_1^-}{dx} + \frac{1}{\tau_1}\left(\frac{t_2^+}{2} + \frac{t_2^-}{2} - t_1^-\right) = -1 \tag{54}$$

$$V \frac{dt_2^+}{dx} + \frac{1}{\tau_2}\left(\frac{t_1^+}{2} + \frac{t_1^-}{2} - t_2^+\right) = -1 \tag{55}$$

$$-V \frac{dt_2^-}{dx} + \frac{1}{\tau_2}\left(\frac{t_1^+}{2} + \frac{t_1^-}{2} - t_2^-\right) = -1. \tag{56}$$

Defining $t_i^d = \frac{t_i^+ - t_i^-}{2}$ and $t_i = \frac{t_i^+ + t_i^-}{2}$, we get the following equations (and similar expressions with $v_l \to V$, $t_1 \to t_2$, $t_2 \to t_1$) :

$$v_l \frac{dt_1^d}{dx} + \frac{1}{\tau_1}(t_2 - t_1) = -1 \tag{57}$$

$$v_l \frac{dt_1}{dx} - \frac{1}{\tau_1} t_1^d = 0, \tag{58}$$

which eventually lead to the following system :

$$v_l^2 \tau_1 \frac{d^2 t_1}{dx^2} + \frac{1}{\tau_1}(t_2 - t_1) = -1 \tag{59}$$

$$V^2 \tau_2 \frac{d^2 t_2}{dx^2} + \frac{1}{\tau_2}(t_1 - t_2) = -1, \tag{60}$$

together with :

$$t_1^d = v_l \tau_1 \frac{dt_1}{dx} \tag{61}$$

$$t_2^d = V \tau_2 \frac{dt_2}{dx}. \tag{62}$$

Inside the target $(x \leq a)$, one has $t_1^{+,in}(x) = t_1^{-,in}(x) = 0$, and :

$$V \frac{dt_2^{+,in}}{dx} - \frac{1}{\tau_2} t_2^{+,in} = -1 \tag{63}$$

$$-V \frac{dt_2^{-,in}}{dx} - \frac{1}{\tau_2} t_2^{-,in} = -1. \tag{64}$$

Finally, the boundary conditions read :

$$\left.\frac{dt_2}{dx}\right|_{x=b} = 0 \tag{65}$$

$$\left.\frac{dt_1}{dx}\right|_{x=b} = 0 \tag{66}$$

$$t_2^+(a) = t_{2,in}^+(a) \tag{67}$$

$$t_2^-(a) = t_{2,in}^-(a) \tag{68}$$

$$\left.\frac{dt_{2,in}}{dx}\right|_{x=0} = 0 \tag{69}$$

$$t_1^-(a) = 0 \tag{70}$$

2. Results

The exact expression of t_m (cf. appendix VII B) is obtained through lengthy but standard calculations. To simplify this expression, we consider the small density limit $a/b \to 0$ and finally obtain the following very good approximation of t_m (Fig.7) :

$$t_m = \frac{(\tau_1+\tau_2)b}{\alpha^{3/2}}\left(\left(\frac{b}{3}+L_1\right)\sqrt{\alpha}+\Gamma L_2(\sqrt{\alpha}+L_2)\right) \tag{71}$$

where :

$$\Gamma = \frac{(\sqrt{\alpha}-L_1)(L_1+L_2)+\sqrt{\alpha}(L_2-L_1+\sqrt{\alpha})X+X^2L_2(L_2-L_1)}{((L_1+\sqrt{\alpha})X^2+(L_1-\sqrt{\alpha}))(\sqrt{\alpha}+L_2-L_1)} \tag{72}$$

$$X = e^{\frac{2a}{L_2}} \tag{73}$$

$$\alpha = L_1^2+L_2^2 \tag{74}$$

$$L_2 = V\tau_2 \tag{75}$$

$$L_1 = v_l\tau_1 \tag{76}$$

	$v_l=1$	$v_l=0.1$	$v_l=0.01$	$v_l=0.001$	$\tau_2^{opt,th}(81)$
$b=5$	$\tau_1\to\infty$	$\tau_1\to 0,\ \tau_2^{opt}=0.86$			$\tau_2^{opt,th}=0.91$
$b=50$	$\tau_1\to\infty$		$\tau_1\to 0,\ \tau_2^{opt}=2.9$		$\tau_2^{opt,th}=2.9$
$b=500$	$\tau_1\to\infty$		$\tau_1\to 0,\ \tau_2^{opt}=9.1$		$\tau_2^{opt,th}=9.1$
$b=5000$	$\tau_1\to\infty$			$\tau_1\to 0,\ \tau_2^{opt}=29$	$\tau_2^{opt,th}=29$

Table I: Ballistic mode in 1 dimension. Numerical minimization of the exact t_m (200). Values of τ_1 and τ_2 at the minimum. Comparison with theoretical τ_2. $a=0.5$, $V=1$.

A numerical analysis indicates (Fig.7, Table I) that, depending on the parameters, there are two possible optimal strategies :

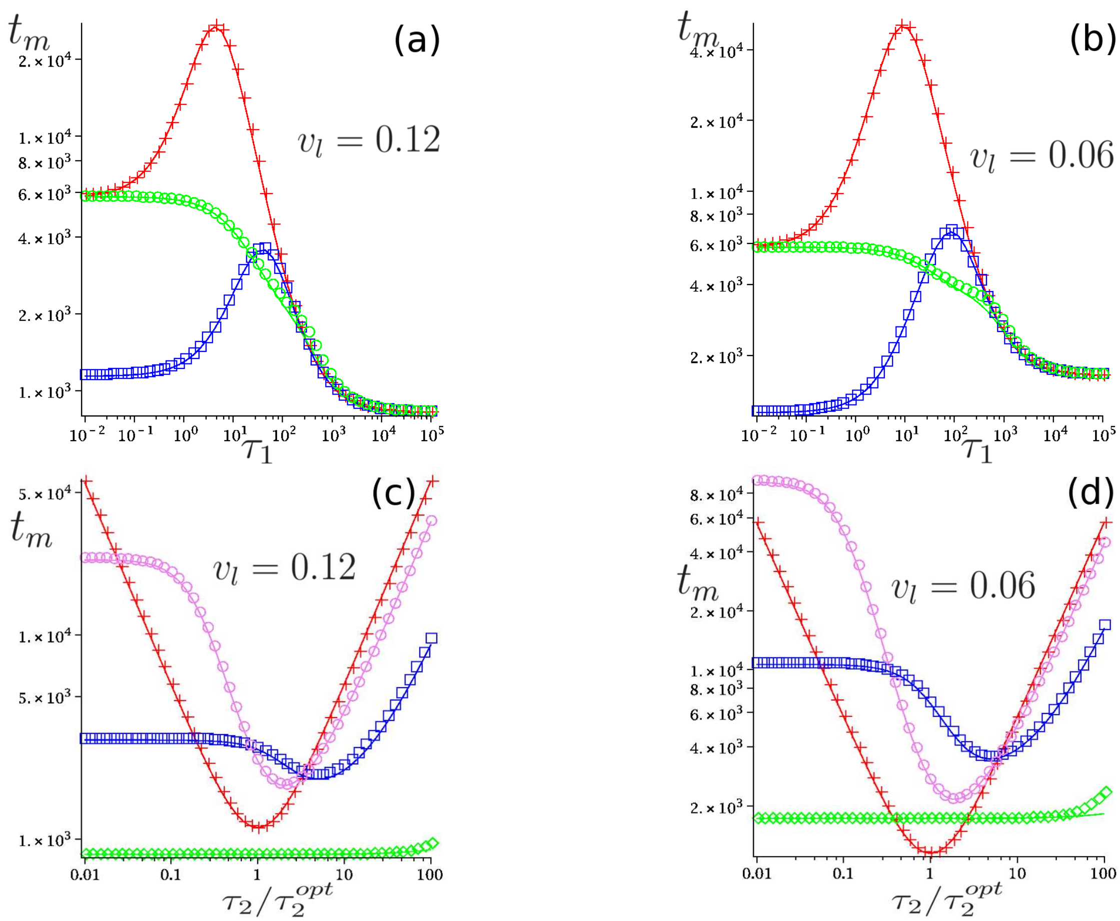

Figure 7: (Color online) Ballistic mode in 1 dimension. Comparison between low density approximation (71) (symbols) and the exact expression of t_m (200) (line). (a), (b) : t_m as a function of τ_1, with $\tau_2 = 0.1\tau_2^{opt}$ (red, crosses), $\tau_2 = \tau_2^{opt}$ (blue, squares), $\tau_2 = 10\tau_2^{opt}$ (green, circles). (c), (d) : t_m as a function of τ_2/τ_2^{opt}, with $\tau_1 = 0$ (red, crosses), $\tau_1 = 10$ (violet, circles), $\tau_1 = 100$ (blue, squares), $\tau_1 = 10000$ (green, diamonds). (a), (c) : $v_l = 0.12 > v_l^c$: intermittence is not favorable. (b), (d) : $v_l = 0.06 < v_l^c$: intermittence is favorable. τ_2^{opt} is from the analytical prediction (81). $a = 1$, $V = 1$, $b = 100$.

- $\tau_1 \to \infty$. Intermittence is not favorable.
- $\tau_1 \to 0, \tau_2 = \tau_2^{opt}$. Intermittence is favorable.

We now study analytically these regimes.

3. *Regime without intermittence :* $\tau_1 \to \infty$

In this regime, there is no intermittence. The searcher starts either inside the target (x in $[-a, a]$) and immediately finds the target, or it starts at a position x outside the target. We can therefore take $x \in [a, b]$. If the searcher goes in the $-x$ direction, it find its target after $T = (x - a)/v_l$. If the searcher goes in the $+x$ direction, it finds its target after $T = ((b - x) + (b - a))/v_l$. This leads to :

$$t_{bal} = \frac{1}{b} \int_a^b \frac{b-a}{v_l} dx = \frac{(b-a)^2}{b v_l}. \tag{77}$$

4. *Intermittent regime*

We take the limit $\tau_1 \to 0$ in the expression of t_m (71) and obtain :

$$\lim_{\tau_1 \to 0} t_m = \frac{b}{V} \left(\frac{b}{3L_2} + \frac{e^{\frac{2a}{L_2}} + 1}{e^{\frac{2a}{L_2}} - 1} \right) \tag{78}$$

Taking the derivative with respect to L_2 yields :

$$\frac{d}{dL_2} \left(\lim_{\tau_1 \to 0} t_m \right) \propto 12ae^{\frac{2a}{L_2}} + 2be^{\frac{2a}{L_2}} - b - be^{\frac{4a}{L_2}} \tag{79}$$

which has only one positive root :

$$L_2^{opt} = \frac{2a}{\ln \left(1 + 6a/b + 2\sqrt{3a/b + 9a^2/b^2} \right)}. \tag{80}$$

In the limit $b \gg a$ it leads to :

$$\tau_2^{opt} = \frac{a}{3V} \sqrt{\frac{b}{a}}, \tag{81}$$

which is in agreement with numerical minimization of the exact mean detection time shown in the table I.

The mean first passage time at the target is minimized in the intermittent regime for $\tau_1 \to 0$ and $\tau_2 = \tau_2^{opt}$. We replace τ_2 by (81) in the expression (78), and take $b \gg a$ to finally obtain :

$$t_m^{opt} = \frac{2}{\sqrt{3}} \frac{b}{V} \sqrt{\frac{b}{a}} \tag{82}$$

$$gain = \frac{\sqrt{3}}{2} \frac{V}{v_l} \sqrt{\frac{a}{b}}. \tag{83}$$

This shows that the gain is larger than 1 for $v_l < v_l^c = V \frac{\sqrt{3}}{2} \sqrt{\frac{a}{b}}$, which defines the regime where intermittence is favorable.

5. Summary

In the case where the phase 1 is modeled by the ballistic mode in dimension 1, we calculated the exact mean first passage time t_m at the target. t_m can be minimized as a function of τ_1 and τ_2, yielding two possible optimal strategies :

- for $v_l > v_l^c = V\frac{\sqrt{3}}{2}\sqrt{\frac{a}{b}}$, intermittence is not favorable : $\tau_1^{opt} \to \infty$, $\tau_2^{opt} \to 0$
- for $v_l < v_l^c = V\frac{\sqrt{3}}{2}\sqrt{\frac{a}{b}}$, intermittence is favorable, with $\tau_1^{opt} \to 0$ and $\tau_2^{opt} = \frac{a}{3V}\sqrt{\frac{b}{a}}$

Note that the model studied in [2] shows that when targets are not revisitable, the optimal strategy for a 1 state searcher is to perform a straight ballistic motion. This strategy corresponds to $\tau_1 \to \infty$ in our model. Our results show that if a faster phase without detection is allowed, this straight line strategy can be outperformed.

D. Conclusion in dimension 1

Intermittent search strategies in dimension 1 share similar features for the static, diffusive and ballistic detection modes. In particular, all modes show regimes where intermittence is favorable and lead to a minimization of the search time. Strikingly, the optimal duration of the non-reactive relocation phase 2 is quite independent of the modeling of the reactive phase : $\tau_2^{opt} = \frac{a}{3V}\sqrt{\frac{b}{a}}$ for the static mode, for the ballistic mode (in the regime $v_l < v_l^c \simeq \frac{V}{2}\sqrt{\frac{3a}{b}}$), and for the diffusive mode (in the regime $b > \frac{D}{V}$ and $a \gg \frac{D}{V}\sqrt{\frac{b}{a}}$). This shows the robustness of the optimal value τ_2^{opt}.

IV. DIMENSION 2

The 2-dimensional problem is particularly well suited to model animal behaviors. It is also relevant to the microscopic scale, since it mimics for example the case of cellular traffic on membranes [25]. The results for the static and diffusive modes, already treated in [8, 9], are summarized here for completeness. While in dimension 1 the mean search time can be calculated analytically, we introduce in dimension 2 (and later dimension 3) approximation schemes, which we check by numerical simulations. In these numerical simulations, diffusion was simulated using variable step lengths, as in [38], and we used square domains instead of

disks for numerical convenience (it was checked numerically that results are not affected as soon as $b \gg a$).

A. Static mode

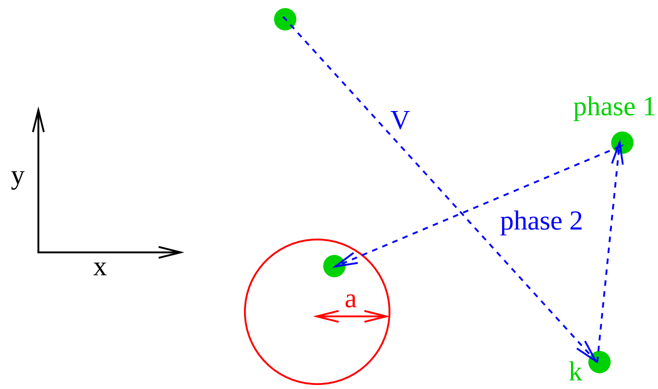

Figure 8: (Color online) Static mode in dimension 2

We study here the case where the detection phase is modeled by the static mode : the searcher does not move during the detection phase and has a finite reaction rate with the target if it is within its detection radius a.

1. Equations

The mean first passage time (MFPT) at a target satisfies the following backward equations [39]:

$$\frac{1}{2\pi\tau_1}\int_0^{2\pi}(t_2(\overrightarrow{r}) - t_1(\overrightarrow{r}))d\theta_{\overrightarrow{V}} - k\mathrm{I}_a(\overrightarrow{r})t_1(\overrightarrow{r}) = -1. \tag{84}$$

$$\overrightarrow{V}\cdot\nabla_{\mathbf{r}}t_2(\overrightarrow{r}) - \frac{1}{\tau_2}(t_2(\overrightarrow{r}) - t_1(\overrightarrow{r})) = -1 \tag{85}$$

The function I_a is defined by $\mathrm{I}_a(\overrightarrow{r}) = 1$ inside the target (if $|\overrightarrow{r}| \leq a$) and $\mathrm{I}_a(\overrightarrow{r}) = 0$ outside the target (if $|\overrightarrow{r}| > a$). In the present form, these integro-differential equations (completed with boundary conditions) do not seem to allow for an exact resolution with standard methods. t_2 is the mean first passage time on the target, starting from $\overrightarrow{r}$ in phase 2, with speed $\overrightarrow{V}$, of angle θ_v, and with projections on the axes V_x, V_y. i and j can take

either x or y as a value. We use the following decoupling assumption :

$$\langle V_i V_j t_2 \rangle_{\theta_{\mathbf{V}}} \simeq \langle V_i V_j \rangle_{\theta_{\mathbf{V}}} \langle t_2 \rangle_{\theta_{\mathbf{V}}} \tag{86}$$

and finally obtain the following approximation of the mean search time, which can be checked by numerical simulations :

$$t_m = \frac{\tau_1+\tau_2}{2k\tau_1 y^2}\left\{\frac{1}{x}(1+k\tau_1)(y^2-x^2)^2\frac{\mathrm{I}_0(x)}{\mathrm{I}_1(x)} + \frac{1}{4}\left[8y^2 + (1+k\tau_1)\left(4y^4\ln(y/x) + (y^2-x^2)(x^2-3y^2+8)\right)\right]\right\} \tag{87}$$

$$\text{where } x = \sqrt{\frac{2k\tau_1}{1+k\tau_1}}\frac{a}{V\tau_2} \text{ and } y = \sqrt{\frac{2k\tau_1}{1+k\tau_1}}\frac{b}{V\tau_2} \tag{88}$$

In that case, intermittence is trivially necessary to find the target: indeed, if the searcher does not move, the MFPT is infinite. In the regime $b \gg a$, the optimization of the search time (87) leads to :

$$\tau_1^{opt} = \left(\frac{a}{Vk}\right)^{1/2}\left(\frac{2\ln(b/a)-1}{8}\right)^{1/4}, \tag{89}$$

$$\tau_2^{opt} = \frac{a}{V}\left(\ln(b/a)-1/2\right)^{1/2}, \tag{90}$$

and the minimum search time is given in the large volume limit by :

$$\begin{aligned} t_m^{opt} &= \frac{b^2}{a^2k} - \frac{2^{1/4}}{\sqrt{Vka^3}}\frac{(a^2-4b^2)\ln(b/a)+2b^2-a^2}{(2\ln(b/a)-1)^{3/4}} \\ &-\frac{\sqrt{2}}{48ab^2V}\frac{(96a^2-192b^4)\ln^2(b/a)+(192b^4-144a^2b^2)\ln(b/a)+46a^2b^2-47b^4+a^4}{(2\ln(b/a)-1)^{3/2}} \end{aligned} \tag{91}$$

2. Summary

In the case of a static detection mode in dimension 2, we obtained a simple approximate expression of the mean first passage time t_m at the target. With the static detection mode, intermittence is always favorable and leads to a single optimal intermittent strategy. The minimal search time is realized for $\tau_1^{opt} = \left(\frac{a}{Vk}\right)^{1/2}\left(\frac{2\ln(b/a)-1}{8}\right)^{1/4}$ and $\tau_2^{opt} = \frac{a}{V}\left(\ln(b/a)-1/2\right)^{1/2}$. Importantly, the optimal duration of the relocation phase does not depend on k, i.e. on the description of the detection phase, as in dimension 1.

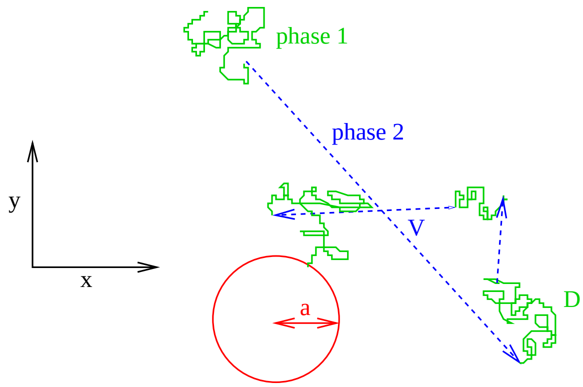

Figure 9: (Color online) Diffusive mode in dimension 2

B. Diffusive mode

We now assume that the searcher diffuses during the detection phase. For this process, the mean first passage time at the target satisfies the following backward equation [39]:

$$D\nabla^2_{\mathbf{r}} t_1(\overrightarrow{r}) + \frac{1}{2\pi\tau_1}\int_0^{2\pi}(t_2(\overrightarrow{r}) - t_1(\overrightarrow{r}))d\theta_{\mathbf{V}} = -1 \tag{92}$$

$$\overrightarrow{V}\cdot\nabla_{\mathbf{r}} t_2(\overrightarrow{r}) - \frac{1}{\tau_2}(t_2(\overrightarrow{r}) - t_1(\overrightarrow{r})) = -1 \tag{93}$$

with $t_1(\overrightarrow{r}) = 0$ inside the target ($r \leq a$). We use the same decoupling assumption than for the static case (86). It eventually leads to the following approximation of the mean search time :

$$t_m = (\tau_1+\tau_2)\frac{1-a^2/b^2}{(\alpha^2 D\tau_1)^2}\left\{a\alpha(b^2/a^2-1)\frac{M}{2L_+} - \frac{L_-}{L_+} - \frac{\alpha^2 D\tau_1}{8\widetilde{D}\tau_2}\frac{(3-4\ln(b/a))b^4 - 4a^2b^2 + a^4}{b^2-a^2}\right\}, \tag{94}$$

with $L_\pm = \mathrm{I}_0\left(\frac{a}{\sqrt{\widetilde{D}\tau_2}}\right)(\mathrm{I}_1(b\alpha)\mathrm{K}_1(a\alpha) - \mathrm{I}_1(a\alpha)\mathrm{K}_1(b\alpha)) \pm \alpha\sqrt{\widetilde{D}\tau_2}\,\mathrm{I}_1\left(\frac{a}{\sqrt{\widetilde{D}\tau_2}}\right)(\mathrm{I}_1(b\alpha)\mathrm{K}_0(a\alpha) + \mathrm{I}_0(a\alpha)\mathrm{K}_1($

and $M = \mathrm{I}_0\left(\frac{a}{\sqrt{\widetilde{D}\tau_2}}\right)(\mathrm{I}_1(b\alpha)\mathrm{K}_0(a\alpha) + \mathrm{I}_0(a\alpha)\mathrm{K}_1(b\alpha)) - 4\frac{a^2\sqrt{\widetilde{D}\tau_2}}{\alpha(b^2-a^2)^2}\mathrm{I}_1\left(\frac{a}{\sqrt{\widetilde{D}\tau_2}}\right)(\mathrm{I}_1(b\alpha)\mathrm{K}_1(a\alpha) - \mathrm{I}_1(a\alpha)\mathrm{K}$

where $\alpha = (1/(D\tau_1) + 1/(\widetilde{D}\tau_2))^{1/2}$ and $\widetilde{D} = v^2\tau_2$. We then minimize this time as a function of τ_1 and τ_2.

1. $a < b \ll D/V$: *intermittence is not favorable*

In that regime, intermittence is not favorable. Indeed, the typical time required to explore the whole domain of radius b is of order b^2/D for a diffusive motion, which is shorter than the corresponding time b/V for a ballistic motion. As a consequence, it is never useful to interrupt the diffusive phases by mere relocating ballistic phases. We use standard methods to calculate the mean first passage time at the target in this optimal regime of diffusion only :

$$\frac{D}{r}\frac{d}{dr}\left(r\frac{dt}{dr}\right) = -1 \tag{95}$$

The boundary conditions $t(a) = 0$ and $\frac{dt}{dr}(r = b) = 0$ lead to :

$$t_{diff} = \frac{1}{8b^2 D_{eff}}\left(4a^2b^2 - a^4 - 3b^4 + 4b^4 \ln\frac{b}{a}\right), \tag{96}$$

and we find in the limit $b \gg a$:

$$t_{diff} = \frac{b^2}{8D_{eff}}\left(-3 + 4\ln\frac{b}{a}\right) \tag{97}$$

2. $a \ll D/V \ll b$: *first regime of intermittence*

In this second regime, one can use the following approximate formula for the search time:

$$t_m = \frac{b^2}{4DV^2\alpha^2}\frac{\tau_1 + \tau_2}{\tau_1\tau_2^2}\left\{4\ln(b/a) - 3 - 2\frac{(V\tau_2)^2}{D\tau_1}(\ln(\alpha a) + \gamma - \ln 2)\right\}, \tag{98}$$

γ being the Euler constant. An approximate criterion to determine if intermittence is useful can be obtained by expanding t_m in powers of $1/\tau_1$ when $\tau_1 \to \infty$ ($\tau_1 \to \infty$ corresponds to the absence of intermittence), and requiring that the coefficient of the term $1/\tau_1$ is negative for all values of τ_2. Using this criterion, we find that intermittence is useful if

$$\sqrt{2}\exp(-7/4 + \gamma)Vb/D - 4\ln(b/a) + 3 > 0, \tag{99}$$

In this regime, using Eq(98), the optimization of the search time leads to

$$\tau_1^{opt} = \frac{b^2}{D}\frac{4\ln w - 5 + c}{w^2(4\ln w - 7 + c)}, \quad \tau_2^{opt} = \frac{b}{V}\frac{\sqrt{4\ln w - 5 + c}}{w} \tag{100}$$

where w is the solution of the implicit equation $w = 2Vbf(w)/D$ with

$$\frac{\sqrt{4\ln w - 5 + c}}{f(w)} = -8(\ln w)^2 + (6 + 8\ln(b/a))\ln w - 10\ln(b/a) + 11 - c(c/2 + 2\ln(a/b) - 3/2) \tag{101}$$

and $c = 4(\gamma - \ln(2))$, γ being the Euler constant. A useful approximation for w is given by

$$w \simeq \frac{2Vb}{D} f\left(\frac{Vb}{2D\ln(b/a)}\right). \tag{102}$$

The gain for this optimal strategy reads :

$$gain = \frac{t_{diff}}{t_m^{opt}} \simeq \frac{1}{2}\frac{4\ln b/a - 3 + 4a^2/b^2 - a^4/b^4}{4\ln b/a - 3 + 2(4\ln w)\ln(b/aw)}\left(\frac{1}{4\ln w - 5} + \frac{wD}{bV}\frac{4\ln w - 7}{(4\ln w - 5)^{3/2}}\right)^{-1} \tag{103}$$

If intermittence significantly speeds up the search in this regime (typically by a factor 2), it does not change the order of magnitude of the search time.

3. $D/V \ll a \ll b$: *"universal" regime of intermittence*

In the last regime $D/V \ll a \ll b$, the optimal strategy is obtained for

$$\tau_1^{opt} \simeq \frac{D}{2V^2}\frac{\ln^2(b/a)}{2\ln(b/a) - 1},\ \tau_2^{opt} \simeq \frac{a}{V}(\ln(b/a) - 1/2)^{1/2} \tag{104}$$

and the gain reads:

$$gain = \frac{t_{diff}}{t_m^{opt}} \simeq \frac{\sqrt{2}aV}{8D}\left(\frac{1}{4\ln(b/a) - 3}\frac{\mathrm{I}_0\left(2/\sqrt{2\ln(b/a) - 1}\right)}{\mathrm{I}_1\left(2/\sqrt{2\ln(b/a) - 1}\right)} + \frac{1}{2\sqrt{2\ln(b/a) - 1}}\right)^{-1} \tag{105}$$

Here, the optimal strategy leads to a significant decrease of the search time which can be rendered arbitrarily smaller than the search time in absence of intermittence.

4. *Summary*

We studied the case where the detection phase 1 is modeled by a diffusive mode, and obtained an approximation of the mean first passage time at the target. We found that intermittence is favorable (i.e. better than diffusion alone), in the regime of large system size $b \gg D/V$. The optimal intermittent strategy then follows two subregimes :

- if $a \ll D/V$, the best strategy is given by (100). The search is significantly reduced by intermittence but keeps the same order of magnitude as in the case of a 1-state diffusive search.

- if $a \gg D/V$, the best strategy is given by (104), and weakly depends on b. In this regime, intermittence is very efficient as shown by the large gain obtained for V large.

C. Ballistic mode

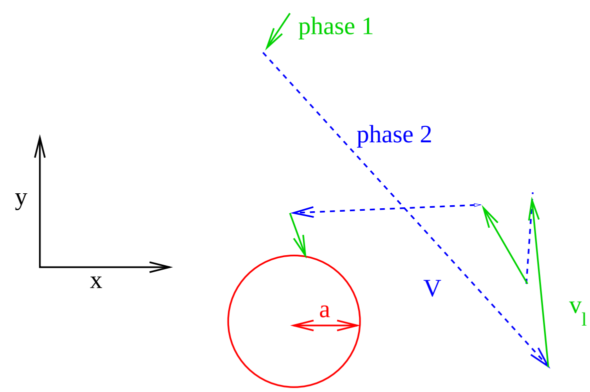

Figure 10: (Color online) Ballistic mode in two dimensions

In this case, the searcher has access to two different speeds: one (V) is fast but prevents target detection, and the other one (v_l) is slower but enables target detection.

1. Simulations

Since an explicit expression of the mean search time is not available, a numerical study is performed. Exploring the parameter space numerically enables to identify the regimes where the mean search time is minimized. Then, for each regime, approximation schemes are developed to provide analytical expression of the mean search time.

The numerical results presented in figure 11 suggest two regimes defined according to a threshold value v_l^c of v_l to be determined later on :

- for $v_l > v_l^c$, t_m is minimized for $\tau_2 \to 0$
- for $v_l < v_l^c$, t_m is minimized for $\tau_1 \to 0$.

2. Regime without intermittence ($\tau_2 \to 0$, $\tau_1 \to \infty$)

Qualitatively, it is rather intuitive that for v_l large enough (the precise threshold value v_l^c will be determined next), phase 2 is inefficient since it does not allow for target detection. The optimal strategy is therefore $\tau_2 \to 0$ in this case. In this regime, the searcher performs

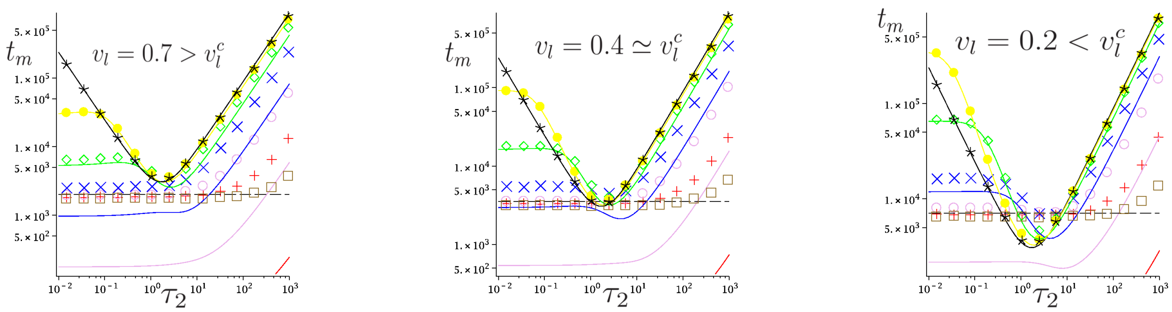

Figure 11: (Color online) Ballistic mode in 2 dimensions. $\ln(t_m)$ as a function of $\ln(\tau_2)$. Simulations (symbols), diffusive/diffusive approximation (94) with (109) (colored lines), $\tau_1 \to 0$ limit (110) (black line), $\tau_1 \to \infty$ (no intermittence) (108) (dotted black line). $b = 30$, $a = 1$, $V = 1$. $\tau_1 = 0$ (black, stars), $\tau_1 = 0.17$ (yellow, solid circles), $\tau_1 = 0.92$ (green, diamonds), $\tau_1 = 5.0$ (blue, X), $\tau_1 = 28$ (purple, circles), $\tau_1 = 150$ (red, +), $\tau_1 = 820$ (brown, squares).

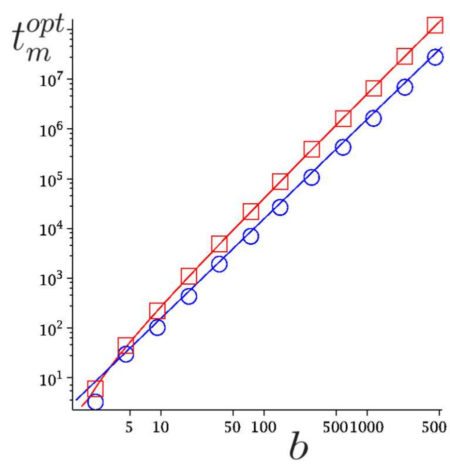

Figure 12: (Color online) Ballistic mode in 2 dimension. t_m^{opt} as a function of b, logarithmic scale. Regime without intermittence ($\tau_2 = 0$ and $\tau_1 \to \infty$, $v_l = 1$), analytical approximation (108) (blue line), numerical simulations (blue circles). Regime with intermittence (with $\tau_1 = 0$, $V = 1$), analytical approximation (112) (red line), numerical simulations (red squares). $a = 1$

a ballistic motion, which is randomly reoriented with frequency $1/\tau_1$. Along the same line as in [2] (where however the times between successive reorientations are Levy distributed), it can be shown that the optimal strategy to find a target (which is assumed to disappear after the first encounter) is to minimize oversampling and therefore to perform a purely ballistic motion. In our case this means that in this regime $\tau_2 \to 0$, the optimal τ_1 is given by $\tau_1^{opt} \to \infty$.

In this regime, we can propose an estimate of the optimal search time t_{bal}. The surface scanned during δt is $2av_l\delta t$. $p(t)$ is the proportion of the total area which has not yet been scanned at t. If we neglect correlations in the trajectory, one has :

$$\frac{dp}{dt} = -\frac{2av_l p(t)}{\pi b^2}. \tag{106}$$

Then, given that $p(t=0)=1$, we find

$$p(t) = \exp\left(-\frac{2av_l}{\pi b^2}\right), \tag{107}$$

and the mean first passage time at the target in these conditions is :

$$t_{bal} = -\int_0^\infty t\frac{dp}{dt}dt = \frac{\pi b^2}{2av_l}. \tag{108}$$

This expression yields (Fig.12) a good agreement with numerical simulations. Note in particular that $t_{bal} \propto \frac{1}{v_l}$.

3. *Regime with intermittence* $\tau_1 \to 0$

In this regime where $v_l < v_l^c$, the numerical study shows that the search time is minimized for $\tau_1 \to 0$ (Fig.11). We here determine the optimal value of τ_2 in this regime. To proceed we approximate the problem by the case of a diffusive mode previously studied (94), with an effective diffusion coefficient :

$$D = \frac{v_l^2\tau_1}{2}. \tag{109}$$

This approximation is very satisfactory in the regime $\tau_1 \to 0$ as shown in Fig.11.

We can then use the results of [8, 9] in the $\tau_1 \to 0$ regime and obtain:

$$t_m = \tau_2\left(1-\frac{a^2}{b^2}\right)\left(1-\frac{1}{4}\frac{\left(3+4\ln\left(\frac{a}{b}\right)\right)b^4-4a^2b^2+a^4}{\tau_2^2V^2\left(b^2-a^2\right)}+\frac{a}{V\tau_2\sqrt{2}}\left(\frac{b^2}{a^2}-1\right)\frac{I_0\left(\frac{a\sqrt{2}}{\tau_2 V}\right)}{I_1\left(\frac{a\sqrt{2}}{\tau_2 V}\right)}\right) \tag{110}$$

The calculation of τ_2^{opt} minimizing t_m then gives:

$$\tau_2^{opt} = \frac{a}{v}\sqrt{\ln\left(\frac{b}{a}\right)-\frac{1}{2}} \tag{111}$$

In turn, replacing τ_2 by τ_2^{opt} (111) in (110), we obtain the minimal mean time of target detection :

$$t_m^{opt} = \frac{a}{u\sqrt{2}V}\left(1-\frac{a^2}{b^2}\right)\left(1-u^2\frac{\left(3+4\ln\left(\frac{a}{b}\right)\right)b^4-4a^2b^2+a^4}{a^2 2\left(b^2-a^2\right)}+\frac{u\left(\frac{b^2}{a^2}-1\right)I_0\left(2u\right)}{I_1\left(2u\right)}\right) \tag{112}$$

with $u = \left(\ln\left(\frac{b}{a}\right)-1\right)^{-\frac{1}{2}}$. It can be noticed that $t_m^{opt} \propto \frac{1}{V}$. Note that if $b \gg a$ this last expression can be greatly simplified:

$$t_m^{opt} \simeq \frac{2b^2}{aV}\sqrt{\ln\left(\frac{b}{a}\right)} \tag{113}$$

Finally the gain reads (using (108) and (113)):

$$gain = \frac{t_{bal}}{t_m^{opt}} \simeq \frac{\pi V}{4v_l}\left(\ln\left(\frac{b}{a}\right)\right)^{-0.5} \tag{114}$$

Numerical simulations of Fig.12 shows the validity of these approximations.

4. *Determination of v_l^c*

It is straightforward than $v_l^c < V$. Indeed, if $v_l = V$, phase 2 is useless, since it prevents target detection. Actually, an estimate of v_l^c can be obtained from (114) as the value of v_l for which $gain = 1$:

$$v_l^c \simeq \frac{\pi V}{4}\left(\ln\left(\frac{b}{a}\right)\right)^{-0.5} \propto \frac{V}{\sqrt{\ln(b/a)}}. \tag{115}$$

We note that this expression (Fig.13) gives the correct dependence on b, but it however departs from the value obtained by numerical simulations. This is due to fact that the expression of t_m^{opt} with intermittence (113) is an under estimate, while t_{bal} given in (108) is an upper estimate. It is noteworthy that intermittence is less favorable with increasing b. This effect is similar to the 1 dimensional case, even though it is less important here. It can be understood as follows: at very large scales the intermittent trajectory is reoriented many times and therefore scales as diffusion, which is less favorable than the non intermittent ballistic motion.

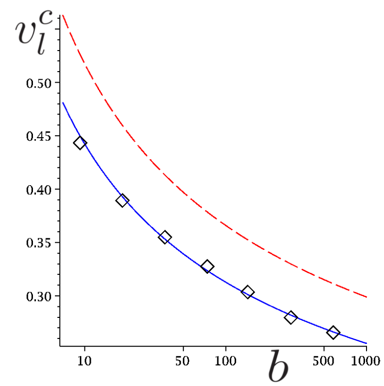

Figure 13: (Color online) Ballistic mode in two dimension. v_l^c as a function of $\ln(b)$ by simulations (symbols), predicted expression (115) (red dotted line), predicted expression multiplied with a fitted numerical constant (blue line). $V = 1$, $a = 1$.

5. *Summary*

We studied the case of ballistic mode in the detection phase 1 in dimension 2. When $v_l > v_l^c$, the optimal strategy is to remain in phase 1 and to explore the domain in a purely ballistic way. Therefore, $\tau_2^{opt} \to 0$, $\tau_1^{opt} \to \infty$. When $v_l < v_l^c$, we find on the contrary $\tau_1^{opt} \to 0$ and $\tau_2^{opt} = \frac{a}{V}\sqrt{\ln\left(\frac{b}{a}\right) - \frac{1}{2}}$. The threshold value is given by $v_l^c \propto \frac{V}{\sqrt{\ln(b/a)}}$ and shows that when the target density decreases, intermittence is less favorable.

D. Conclusion of the 2-dimensional problem

Remarkably, for the three different modes of detection (static, diffusive and ballistic), we find a regime where intermittence permits to minimize the search time for one and the same τ_2^{opt}, given by $\tau_2^{opt} = \frac{a}{V}\sqrt{\ln\left(\frac{b}{a}\right) - \frac{1}{2}}$. As in dimension 1, this indicates that optimal intermittent strategies are robust and widely independent of the details of the description of the detection mechanism.

V. DIMENSION 3

The 3 dimensional case is also relevant to biology. At the microscopic scale, it corresponds for example to intracellular traffic in the bulk cytoplasm of cells, or at larger scales to animals

living in 3 dimensions, such as plankton [40], or *C.elegans* in its natural habitat [41]. As it was the case in dimension 2, different assumptions have to be made to obtain analytical expressions of the search time. We checked the validity of our assumptions with numerical simulations using the same algorithms as in dimension 2.

A. Static mode

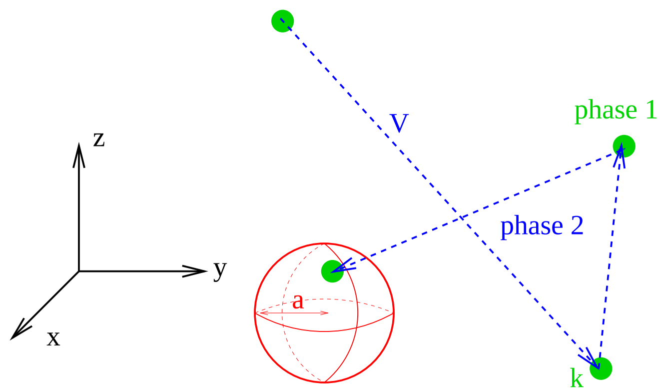

Figure 14: (Color online) Static mode in three dimensions

We study in this section the case where the detection phase is modeled by the static mode, for which the searcher does not move during the detection phase and has a finite reaction rate with the target if it is within a detection radius a.

1. Equations

Denoting $t_1(r)$ the mean first passage time at the target starting from a distance r from the target in phase 1 (detection phase), and $t_{2,\theta,\phi}(r)$ the mean first passage time at the target starting from a distance r from the target in phase 2 (relocation phase) with a direction characterized by θ and ϕ, we get :

$$\overrightarrow{V}.\overrightarrow{\bigtriangledown}t_{2,\theta,\phi} + \frac{1}{\tau_2}\left(t_1 - t_{2,\theta,\phi}\right) = -1. \tag{116}$$

Then one has outside the target $(r > a)$:

$$\frac{1}{\tau_1}\left(\frac{1}{4\pi}\int_0^{\pi} d\theta sin\theta \int_0^{2\pi} d\phi t_{2,\theta,\phi} - t_1\right) = -1, \tag{117}$$

and inside the target $(r \leq a)$:

$$\frac{1}{\tau_1}\frac{1}{4\pi}\int_0^{\pi} d\theta sin\theta \int_0^{2\pi} d\phi t_{2,\theta,\phi} - \left(\frac{1}{\tau_1} + k\right) t_1 = -1. \tag{118}$$

With $t_2 = \frac{1}{4\pi}\int_0^{\pi} d\theta sin\theta \int_0^{2\pi} d\phi t_{2,\theta,\phi}$, we obtain outside the target $(r > a)$:

$$\frac{1}{\tau_1}(t_2 - t_1) = -1 \tag{119}$$

and inside the target $(r < a)$:

$$\frac{1}{\tau_1}t_2 - \left(\frac{1}{\tau_1} + k\right) t_1 = -1. \tag{120}$$

Making a similar decoupling approximation as in dimension 2, we finally get :

$$\frac{V^2\tau_2}{3} \triangle t_2 - \frac{1}{\tau_2}(t_1 - t_2) = -1. \tag{121}$$

We solve these equations for inside and outside the target, using the following boundary conditions :

$$\left.\frac{dt_2^{out}}{dr}\right|_{r=b} = 0 \tag{122}$$

$$t_2^{out}(a) = t_2^{in}(a) \tag{123}$$

$$\left.\frac{dt_2^{out}}{dr}\right|_{r=a} = \left.\frac{dt_2^{in}}{dr}\right|_{r=a} \tag{124}$$

and the condition that $t_2^{in}(0)$ should be finite.

2. *Results*

We find an explicit expression of the mean search time

$$t_m = (\tau_1+\tau_2)\left(\frac{1}{k\tau_1} + \frac{1}{b^3V^2\tau_2^2}\left(-2\,b^3\left(b^2-a^2\right) + \left(b^3-a^3\right)\left(3\,\frac{a^2}{\alpha^2}+\beta\right) + \frac{1}{5}(b^5-a^5)\right)\right) \tag{125}$$

with

$$\beta = \frac{-\sinh(\alpha)\,a^3 + \alpha\,\cosh(\alpha)\,b^3}{a\left(-\sinh(\alpha) + \alpha\,\cosh(\alpha)\right)} \tag{126}$$

and $\alpha = \sqrt{3\frac{k\tau_1}{1+k\tau_1}}\frac{a}{V\tau_2}$.

In the limit $b \gg a$, this can be simplified to :

$$t_m = (\tau_1+\tau_2)\left(\frac{1}{k\tau_1} + \frac{1}{\tau_2^2V^2}\left(\frac{-\sinh(\alpha)\,a^3 + \alpha\,\cosh(\alpha)\,b^3}{a\left(-\sinh(\alpha)+\alpha\,\cosh(\alpha)\right)} - \frac{9}{5}b^2 + \frac{3a^2}{\alpha^2}\right)\right). \tag{127}$$

Assuming further that α is small, we use the expansion $\beta \simeq \frac{b^3}{a}\left(1-\tanh(\alpha)/\alpha\right)^{-1} \simeq \frac{b^3}{a}\left(\frac{3}{\alpha^2}+\frac{6}{5}\right)$ and rewrite mean search time as :

$$t_m = \frac{b^3(\tau_2+\tau_1)}{a}\left(\frac{(1+k\tau_1)}{\tau_1 k a^2}+\frac{6}{5\tau_2^2 V^2}\right). \tag{128}$$

This expression of t_m can be minimized for :

$$\tau_1^{opt} = \left(\frac{3}{10}\right)^{\frac{1}{4}}\sqrt{\frac{a}{Vk}} \tag{129}$$

$$\tau_2^{opt} = \sqrt{1.2}\frac{a}{V}, \tag{130}$$

and the minimum mean search time reads finally:

$$t_m^{opt} = \frac{1}{\sqrt{5}}\frac{1}{k}\frac{b^3}{a^3}\left(\sqrt{\frac{ak}{V}}24^{1/4}+5^{1/4}\right)^2. \tag{131}$$

3. Comparisons with simulations

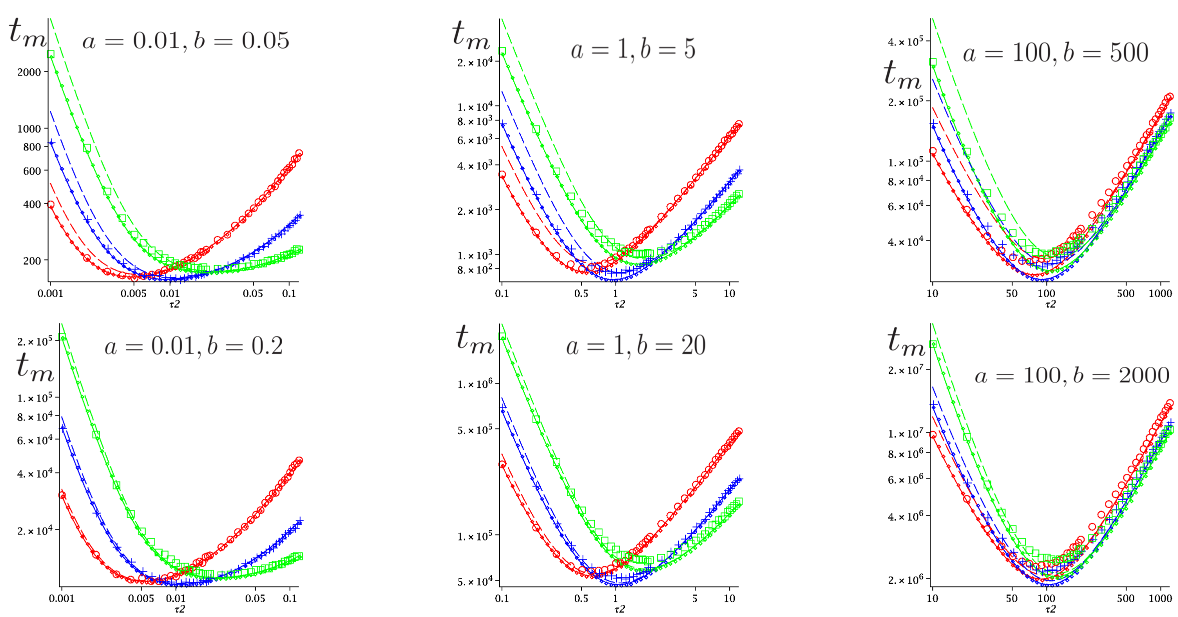

Figure 15: (Color online) Static mode in 3 dimensions. $\ln(t_m)$ as a function of $\ln(\tau_2)$ for different values of τ_1, a and b/a. Comparison between simulations (symbols), analytical expression (125) (line), expression for $b \gg a$ (127) (small dots), and simple expression for $b \gg a$ and α small (128) (dotted line). $\tau_1 \simeq \tau_1^{opt} \simeq 0.74\sqrt{\frac{aV}{k}}$ (129) (blue, crosses), $\tau_1 = 0.25\sqrt{\frac{aV}{k}}$ (red, circles), $\tau_1 = 2.5\sqrt{\frac{aV}{k}}$ (green, squares). $V=1$, $k=1$.

Data obtained by numerical simulations (Fig.15, and additionally in appendix VII C) are in good agreement with the analytical expression (125). In particular, the position of the minimum is very well approximated, and the error on the value of the mean search time at the minimum is close to 10%. Note that the very simple expression (128) fits also rather well the numerical data, except for small τ_2 or small b.

4. Summary

In the case of a static detection mode in dimension 3, we obtained a simple approximate expression of the mean first passage time at the target $t_m = \frac{b^3(\tau_2+\tau_1)}{a}\left(\frac{(1+k\tau_1)}{\tau_1 k a^2} + \frac{6}{5\tau_2^2 V^2}\right)$. t_m has a single minimum for $\tau_1^{opt} = \left(\frac{3}{10}\right)^{\frac{1}{4}}\sqrt{\frac{a}{Vk}}$ and $\tau_2^{opt} = \sqrt{1.2}\frac{a}{V}$, and the minimal mean search time is $\frac{1}{\sqrt{5}}\frac{1}{k}\frac{b^3}{a^3}\left(\sqrt{\frac{ak}{V}}24^{1/4} + 5^{1/4}\right)^2$. With the static detection mode, intermittence is always favorable and leads to a single optimal intermittent strategy. As in dimension 1 and 2, the optimal duration of the relocation phase does not depend on k, i.e. on the description of the detection phase. In addition, this optimal strategy does not depend on the typical distance between targets b.

One can notice than for the static mode in the three cases studied (1, 2, and 3 dimensions), we have the relation : $\tau_1^{opt} = \sqrt{\tau_2^{opt}/(2k)}$. The optimal durations of the two phases are related independently of the dimension.

B. Diffusive mode

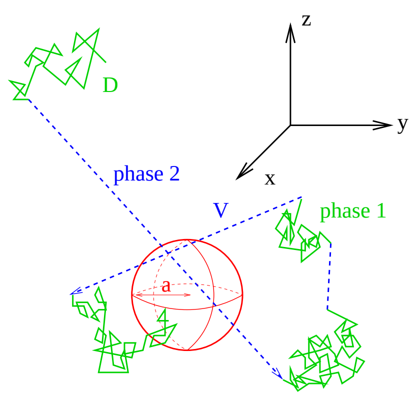

Figure 16: (Color online) Diffusive mode in three dimensions

We now study the case where the detection phase is modeled by a diffusive mode. During the detection phase, the searcher diffuses and detects the target as soon as their respective distance is less than a.

1. *Equations*

One has outside the target $(r > a)$:

$$\overrightarrow{V}.\overrightarrow{\bigtriangledown}t_{2,\theta,\phi} + \frac{1}{\tau_2}\left(t_1 - t_{2,\theta,\phi}\right) = -1 \tag{132}$$

$$D \bigtriangleup t_1 + \frac{1}{\tau_1}\left(\frac{1}{4\pi}\int_0^{\pi} d\theta sin\theta \int_0^{2\pi} d\phi t_{2,\theta,\phi} - t_1\right) = -1 \tag{133}$$

and inside the target $(r \leq a)$:

$$\overrightarrow{V}.\overrightarrow{\bigtriangledown}t_{2,\theta,\phi} - \frac{1}{\tau_2}t_{2,\theta,\phi} = -1 \tag{134}$$

$$t_1 = 0. \tag{135}$$

With $t_2 = \frac{1}{4\pi}\int_0^{\pi} d\theta sin\theta \int_0^{2\pi} d\phi t_{2,\theta,\phi}$, we get outside the target $(r > a)$:

$$D \bigtriangleup t_1^{out} + \frac{1}{\tau_1}\left(t_2^{out} - t_1^{out}\right) = -1 \tag{136}$$

The decoupling approximation described in previous sections then yields outside the target :

$$\frac{V^2\tau_2}{3} \bigtriangleup t_2^{out} + \frac{1}{\tau_2}(t_1^{out} - t_2^{out}) = -1 \tag{137}$$

and inside the target $(r \leq a)$:

$$\frac{V^2\tau_2}{3} \bigtriangleup t_2^{int} - \frac{1}{\tau_2}t_2^{int} = -1. \tag{138}$$

These equations are completed by the following boundary conditions :

$$\left.\frac{dt_2^{out}}{dr}\right|_{r=b} = 0 \tag{139}$$

$$t_2^{out}(a) = t_2^{int}(a) \tag{140}$$

$$\left.\frac{dt_2^{out}}{dr}\right|_{r=a} = \left.\frac{dt_2^{int}}{dr}\right|_{r=a}. \tag{141}$$

2. Results in the general case

Through standard but lengthy calculations we can solve the above system and get an analytical approximation of t_m (cf. appendix VII D 1). In the regime $b \gg a$, we use the assumption $\sqrt{(\tau_1 D)^{-1} + 3(\tau_2 v)^{-2}} \ll b$ and obtain :

$$t_m = \frac{b^3 \kappa_2^4 (\tau_1 + \tau_2)}{\kappa_1} \frac{\tanh(\kappa_2 a) + \frac{\kappa_1}{\kappa_2}}{\kappa_1 \kappa_2^2 \tau_1 D a \left(\tanh(\kappa_2 a) + \frac{\kappa_1}{\kappa_2}\right) - \tanh(\kappa_2 a)} \tag{142}$$

with $\kappa_1 = \frac{\sqrt{\tau 2^2 V^2 + 3\tau_1 D}}{\tau_2 V \sqrt{D\tau_1}}$ and $\kappa_2 = \frac{\sqrt{3}}{V\tau_2}$. As shown in Fig.17 left or in the additional Fig.24 in appendix VII D 2, t_m only weakly depends on τ_1, which indicates that this variable will be less important than τ_2 in the minimization of the search time. The relevant order of magnitude for τ_1^{opt} can be evaluated by comparing the typical diffusion length $L_{diff} = \sqrt{6Dt}$ and the typical ballistic length $L_{bal} = Vt$. An estimate of the optimal time τ_1^{opt} can be given by the time scale for which those lengths are of same order, which gives :

$$\tau_1^{opt} \sim \frac{6D}{V^2}. \tag{143}$$

Note that taking $\tau_1 = 0$ does not change significantly t_m^{opt} (Fig.17 left), and permits to significantly simplify t_m :

$$t_m = \frac{b^3\sqrt{3}}{V^3\tau_2^2}\left(\frac{\sqrt{3}a}{V\tau_2} - \tanh\left(\frac{\sqrt{3}a}{V\tau_2}\right)\right)^{-1} \tag{144}$$

In turn, the minimization of this expression leads to :

$$\tau_2^{opt} = \frac{\sqrt{3}a}{Vx} \tag{145}$$

with x solution of :

$$2\tanh(x) - 2x + x\tanh(x)^2 = 0. \tag{146}$$

This finally yields :

$$\tau_2^{opt} \simeq 1.078\frac{a}{V}. \tag{147}$$

Importantly this approximate expression is very close to the expression obtained for the static mode ($\tau_2^{opt} = \sqrt{\frac{6}{5}}\frac{a}{V} \simeq 1.095\frac{a}{V}$) (130), and there is no dependence with the typical distance between targets b. The simplified expression of the minimal t_m (144) can then be obtained as:

$$t_m^{opt} = \frac{b^3 x^2}{\sqrt{3}a^2 V}\left(x - \tanh(x)\right)^{-1} \simeq 2.18\frac{b^3}{a^2 V} \tag{148}$$

and the gain reads:

$$gain = \frac{t_{diff}}{t_m^{opt}} \simeq 0.15\frac{aV}{D}. \qquad (149)$$

3. Comparison between analytical approximations and numerical simulations

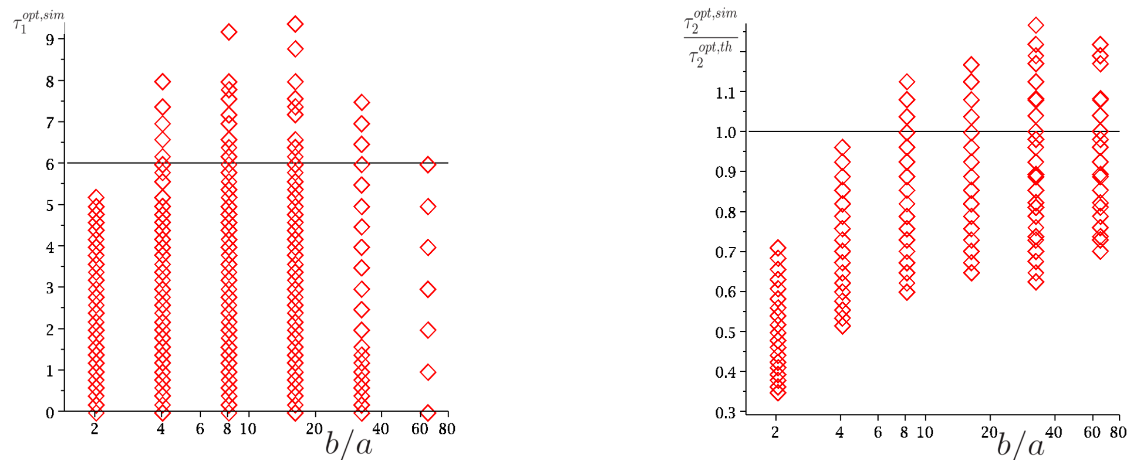

Figure 17: (Color online) Diffusive mode in 3 dimension. Comparison between analytical approximations (143) (145) (black lines) and numerical simulations : the symbols are the values of τ_1 and τ_2 for which $t_m^{simulation} < 1.05 t_m^{opt,simulation}$. $a = 100$, $V = 1$, $D = 1$

Numerical simulations reveal that the minimum of t_m with respect to τ_1 is shallow as it was expected (cf Fig.17 left). It approximately ranges from 0 to the theoretical estimate (143). The value $\tau_2^{opt,sim}$ at the minimum is close to the expected values (145) (cf. Fig.17 right), except for very small b, which is consistent with our assumption $b \gg a$. We can then conclude than the position of the optimum in τ_1 and τ_2 is very well described by the analytical approximations, even if the value of t_m at the minimum is underestimated by our analytical approximation by about 10-20% (Fig.18).

4. Case without intermittence : 1 state diffusive searcher

If the searcher always remains in the diffusive mode, it is straightforward to obtain (cf. appendix VII D 3):

$$t_{diff} = \frac{1}{15Dab^3}\left(5b^3a^3 + 5b^6 - 9b^5a - a^6\right), \qquad (150)$$

which gives in the limit $b/a \gg 1$:

$$t_{diff} = \frac{b^3}{3Da}. \qquad (151)$$

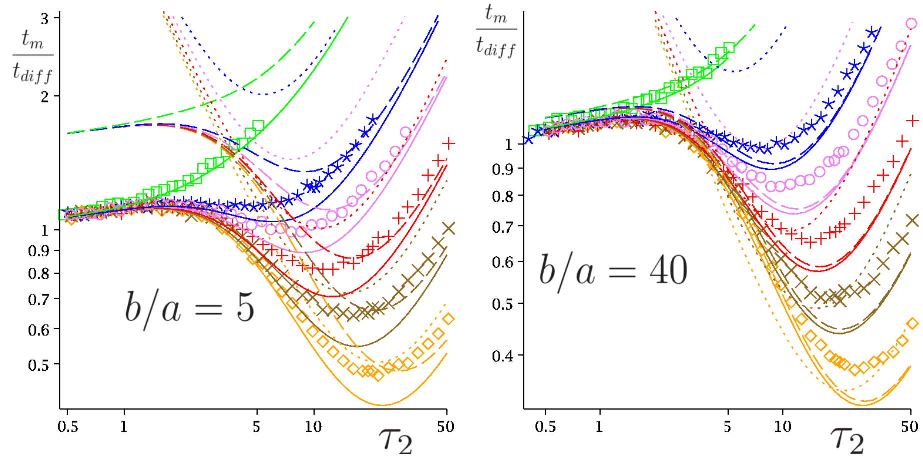

Figure 18: (Color online) Diffusive mode in 3 dimension. t_m/t_{diff} (t_{diff} given by (150)) as a function of τ_2 for different values of the ratio b/a (logarithmic scale). The full analytical form (238) (plain lines) is plotted against the simplified expression (142) (dotted lines), the simplified expression with $\tau_1 = 0$ (144) (small dots), and numerical simulations (symbols) for the following values of the parameters (arbitrary units): $a = 1$ (green, squares), $a = 5$ (blue, stars), $a = 7$ (purple, circles), $a = 10$ (red, $+$), $a = 14$ (brown, X), $a = 20$ (orange, diamonds). $\tau_1 = 6$ everywhere except for the small dots, $v = 1$, $D = 1$. t_m/t_{diff} presents a minimum only for $a > a_c \simeq 4$.

5. *Criterion for intermittence to be favorable*

There is a range of parameters for which intermittence is favorable, as indicated by Fig.18. Both the analytical expression for t_m^{opt} in the regime without intermittence (150) and with intermittence (148) scale as b^3. However, the dependence on a is different (cf. appendix VII D 4). In the diffusive regime, $t_m \propto a^{-1}$, whereas in the intermittent regime $t_m \propto a^{-2}$. This enables to define a critical a_c, such that when $a > a_c$, intermittence is favorable: $a_c \simeq 6.5\frac{D}{V}$ is the value for which the gain (149) is 1.

6. *Summary*

We studied the case where the detection phase 1 is modeled by a diffusive mode, and calculated explicitly an approximation of the mean first passage time at the target. We found that intermittence is favorable (i.e. better than diffusion alone) when $a > a_c \simeq 6.5\frac{D}{V}$:

- if $a < a_c$, the best strategy is a 1 state diffusion, without intermittence, and the mean first passage time at the target is $t_m \simeq \frac{b^3}{3Da}$.

- if $a > a_c$, intermittence is favorable. The dependence on τ_1 is not crucial, as long as it is smaller than $\frac{6D}{V^2}$. The value of τ_2 at the optimum is $\tau_2^{opt} \simeq 1.08\frac{a}{V}$. The minimum search time is then $t_m^{opt} \simeq 2.18\frac{b^3}{a^2V}$.

C. Ballistic mode

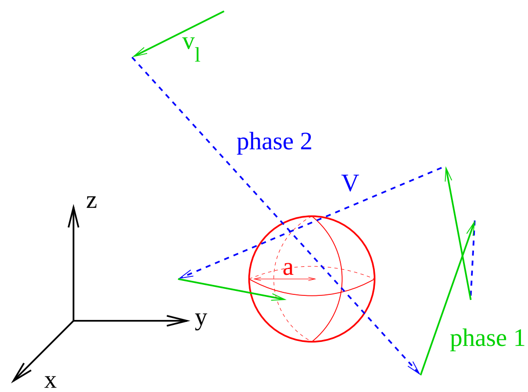

Figure 19: (Color online) Ballistic mode in dimension 3

We now discuss the last case, where the detection phase 1 is modeled by a ballistic mode.Since an explicit analytical determination of the search time seems out of reach, we proceed as in dimension 2 and first explore numerically the parameter space to identify the regimes where the search time can be minimized. We then develop approximation schemes in each regime to obtain analytical expressions (more details are given in appendix VII E).

1. Numerical study

The numerical analysis puts forward two strategies to minimize the search time, depending on a critical value v_l^c to be determined (Fig.20) :

- when $v_l > v_l^c$, $\tau_1^{opt} \to \infty$ and $\tau_2^{opt} \to 0$. In this regime intermittence is not favorable.

- when $v_l < v_l^c$, $\tau_1^{opt} \to 0$, and τ_2^{opt} finite. In this regime the optimal strategy is intermittent.

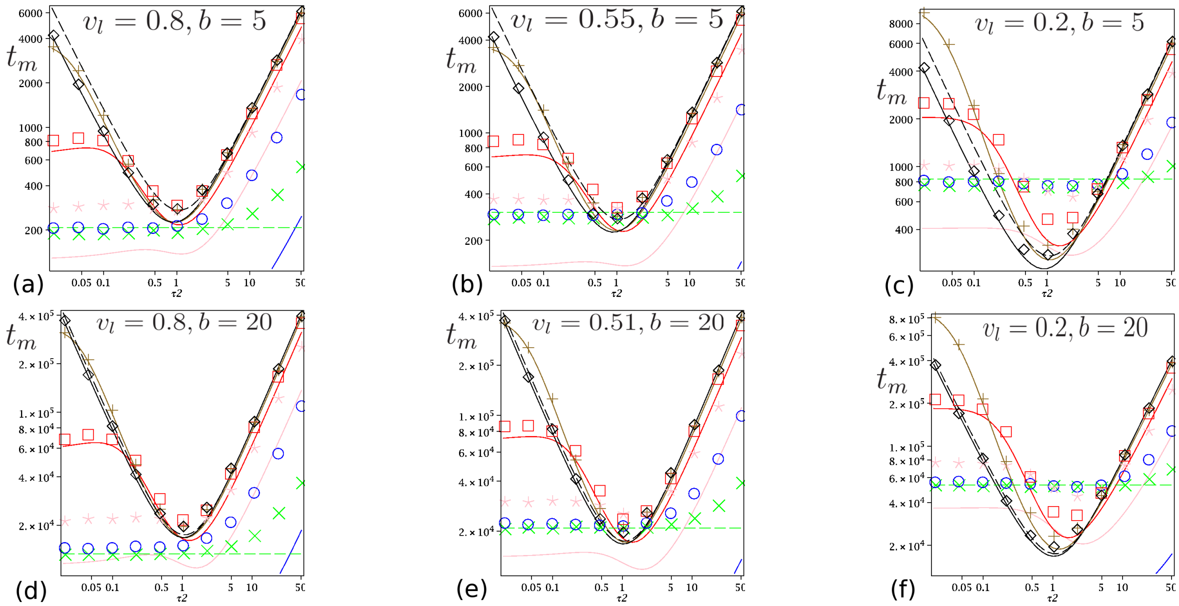

Figure 20: (Color online) Ballistic mode in 3 dimensions. t_m as a function of τ_2 in loglogscale. Simulations (symbols). Approximation $v_l\tau_1 \leq a$ (238 with 253) (colored lines), approximation $\tau_1 = 0$ (153) (black line), approximation $\tau_1 = 0$ and $b \gg a$ (144) (dotted black line). Ballistic limit ($\tau_2 \to 0$ and $\tau_1 \to \infty$) (no intermittence) (152) (green dotted line). (a),(d) : $v_l > v_l^c$, $\tau_{1,1} = 0.04$, $\tau_{1,2} = 0.2$, $\tau_{1,3} = 1$, $\tau_{1,4} = 5$, $\tau_{1,5} = 25$. (b),(e) : $v_l \simeq v_l^c$, $\tau_{1,1} = 0.08$, $\tau_{1,2} = 0.4$, $\tau_{1,3} = 2$, $\tau_{1,4} = 10$, $\tau_{1,5} = 50$. (c),(f) : $v_l < v_l^c$, $\tau_{1,1} = 0.2$, $\tau_{1,2} = 1$, $\tau_{1,3} = 5$, $\tau_{1,4} = 25$, $\tau_{1,5} = 125$. $V = 1$, $a = 1$. $\tau_1 = 0$ (black, diamond), $\tau_1 = \tau_{1,1}$ (brown, +), $\tau_1 = \tau_{1,2}$ (red, squares), $\tau_1 = \tau_{1,3}$ (pink, stars), $\tau_1 = \tau_{1,4}$ (blue, circles), $\tau_1 = \tau_{1,5}$ (green, X)

2. Regime without intermittence (1 state ballistic searcher) : $\tau_2 \to 0$

Following the same argument as in dimension 2, without intermittence the best strategy is obtained in the limit $\tau_1 \to \infty$ (cf. appendix VII E 1) in order to minimize oversampling of the search space. Following the derivation of 108 (see appendix for details), it is found that the search time reads :

$$t_{bal} = \frac{4b^3}{3a^2 v_l}. \tag{152}$$

3. Regime with intermittence

In the regime when intermittence is favorable, the numerical study suggests that the best strategy is realized for $\tau_1 \to 0$ (Fig.20). In this regime $\tau_1 \to 0$, the phase 1 can be well

approximated by a diffusion with effective diffusion coefficient D_{eff} (see (253)). We can then make use of the analytical expression t_m derived in (238). We therefore take $\tau_1 = 0$ in the expression of t_m (238), which yields :

$$t_m(\tau_1 = 0) \simeq \frac{u}{b^3 a V}\left(\frac{\sqrt{3}}{5}\left(5b^3a^2 - 3b^5 - 2a^5\right) + \frac{\left(b^3 - a^3\right)^2 u}{\sqrt{3}a(u - \tanh(u))}\right), \tag{153}$$

where $u = \frac{\sqrt{3}a}{\tau_2 V}$. In the limit $b \gg a$, this expression can be further simplified (see (144)) to :

$$t_m = \frac{b^3\sqrt{3}}{V^2\tau_2^2}\left(\frac{\sqrt{3}a}{V\tau_2} - \tanh\left(\frac{\sqrt{3}a}{V\tau_2}\right)\right)^{-1}, \tag{154}$$

and one finds straightforwardly that $\tau_2^{opt} = \frac{\sqrt{3}a}{Vx}$, where x is solution of $x\tanh(x)^2 + 2\tanh(x) - 2x = 0$, that is $x \simeq 1.606$. Using this optimal value of τ_2 in the expression of t_m (144), we finally get :

$$t_m^{opt} = \frac{2}{\sqrt{3}}\frac{x}{\tanh(x)^2}\frac{b^3}{a^2V} \simeq 2.18\frac{b^3}{a^2V}. \tag{155}$$

These expressions show a good agreement with numerical simulations (Fig.20,Fig.21).

4. *Discussion of the critical value v_l^c*

The gain is given by :

$$gain = \frac{t_{bal}}{t_m^{opt}} \simeq 0.61\frac{V}{v_l}. \tag{156}$$

As in dimension 2, it is trivial that $v_l^c < V$, and the critical value v_l^c can be defined as the value of v_l such that $gain = 1$. This yields

$$v_l^c \simeq 0.6V. \tag{157}$$

Importantly, v_l^c neither depends on b nor a. Simulations are in good agreement with this result (cf. appendix VII E 2), except for a small numerical shift.

5. *Summary*

We studied the case where the detection phase 1 is modeled by a ballistic mode in dimension 3. We have shown by numerical simulations that there are two possible optimal regimes, that we have then studied analytically :

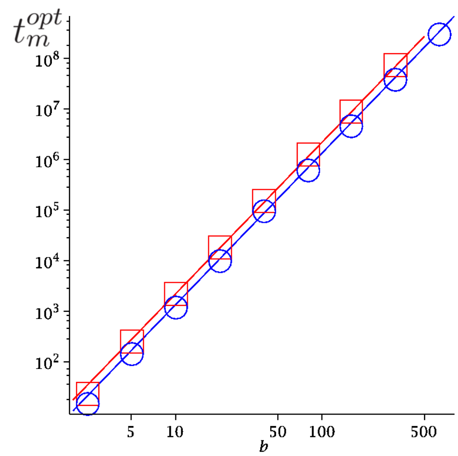

Figure 21: (Color online) Ballistic mode in 3 dimension. t_m^{opt} as a function of b, logarithmic scale. Regime without intermittence ($\tau_2 = 0$ and $\tau_1 \to \infty$, $v_l = 1$), analytical approximation (152) (blue line), numerical simulations (blue circles). Regime with intermittence (with $\tau_1 = 0$, $V = 1$), analytical approximation (155) (red line), numerical simulations (red squares). $a = 1$

- in the first regime $v_l > v_l^c$, the optimal strategy is a 1 state ballistic search ($\tau_1 \to \infty$, $\tau_2 = 0$) and $t_m \simeq \frac{4b^3}{3a^2 v_l}$
- in the second regime $v_l < v_l^c$, the optimal strategy is intermittent ($\tau_1 = 0$, $\tau_2 \simeq 1.1\frac{a}{V}$), and $t_m \simeq 2.18\frac{b^3}{a^2 V}$ (in the limit $b \gg a$).

The critical speed is obtained numerically as $v_l^c \sim 0.5V$ (analytical prediction : $v_l^c \sim 0.6V$). It is noteworthy that when $b \gg a$, the values of τ_1 and τ_2 at the optimum, and the value of v_l^c do not depend on the typical distance between targets b.

D. Conclusion in dimension 3

We found that for the three possible modelings of the detection mode (static, diffusive and ballistic) in dimension 3, there is a regime where the optimal strategy is intermittent. Remarkably, and as was the case in dimension 1 and 2, the optimal time to spend in the fast non-reactive phase 2 is independent of the modeling of the detection mode and reads $\tau_2^{opt} \simeq 1.1\frac{a}{V}$. Additionally, while the mean first passage time on the target scales as b^3, the optimal values of the durations of the two phases do not depend on the target density a/b.

VI. DISCUSSION AND CONCLUSION

The starting point of this paper was the observation that intermittent trajectories are observed in various biological examples of search behaviors, going from the microscopic scale, where searchers can be molecules looking for reactants, to the macroscopic scale of foraging animals. We addressed the general question of determining whether such kind of intermittent trajectories could be favorable from a purely kinetic point of view, that is whether they could allow to minimize the search time for a target. On very general grounds, we proposed a minimal model of search strategy based on intermittence, where the searcher switches between two phases, one slow where detection is possible, the other one faster but preventing target detection. We studied this minimal model in dimensions 1, 2 and 3, and under several modeling hypotheses. We believe that this systematic analysis can be used as a basis to study quantitatively various real search problems involving intermittent behaviors.

More precisely, we calculated the mean first passage time at the target for an intermittent searcher, and minimized this search time as a function of the mean duration of each of the two phases. The table II summarizes the results. In particular, this study shows that for certain ranges of the parameters which we determined, the optimal search strategy is intermittent. In other words, there is an optimal way for the intermittent searcher to tune the mean time it spends in each of the two phases. We found that the optimal durations of the two phases and the gain of intermittent search (as compared to 1 state search) do depend on the target density in dimension 1. In particular, the gain can be very high at low target concentration. Interestingly, this dependence is smaller in dimension 2, and vanishes in dimension 3. The fact that intermittent search is more advantageous in low dimensions (1 and 2) can be understood as follows. At large scale, the intermittent searcher of our model performs effectively a random walk, and therefore scans a space of dimension 2. In an environment of dimension 1 (and critically of dimension 2), the searcher therefore oversamples the space, and it is favorable to perform large jumps to go to previously unexplored areas. On the contrary, in dimension 3, the random walk is transient, and the searcher on average always scans previously unexplored areas, which makes large jumps less beneficial.

Additionally, our results show that, for various modeling choices of the slow reactive phase, there is one and the same optimal duration of the fast non reactive phase, which depends only on the space dimension. This further supports the robustness of optimal intermittent

search strategies. Such robustness and efficiency – and optimality – could explain why intermittent trajectories are observed so often, and in various forms.

Acknowledgement

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	Static mode	Diffusive mode			Ballistic mode	
1D	always intermittence $\tau_1^{opt}=\sqrt{\frac{\tau_2^{opt}}{2k}}\simeq\sqrt{\frac{a}{Vk}}\left(\frac{b}{12a}\right)^{\frac{1}{4}}$ $\tau_2^{opt}\simeq\frac{a}{V}\sqrt{\frac{b}{3a}}$ $t_m^{opt}\simeq\frac{b}{ak}\sqrt{\frac{b}{3a}}\left(\sqrt{\frac{2ka}{V}}+\left(\frac{3a}{b}\right)^{\frac{1}{4}}\right)^2$	$b<\frac{D}{V}$ $\tau_1^{opt}\to\infty$ $\tau_2^{opt}\to 0$ $t_m^{opt}\simeq\frac{b^2}{3D}$	$b>\frac{D}{V}$, $a\ll\sqrt{\frac{b}{a}}\frac{D}{V}$ $\tau_1^{opt}\simeq\left(\frac{b^2D}{36V^4}\right)^{\frac{1}{3}}$ $\tau_2^{opt}\simeq\left(\frac{2b^2D}{9V^4}\right)^{\frac{1}{3}}$ $t_m^{opt}\simeq\left(\frac{3^5b^4}{2^4DV^2}\right)^{\frac{1}{3}}$	$b>\frac{D}{V}$, $a\gg\sqrt{\frac{b}{a}}\frac{D}{V}$ $\tau_1^{opt}\simeq\frac{Db}{48V^2a}$ $\tau_2^{opt}\simeq\frac{a}{V}\sqrt{\frac{b}{3a}}$ $t_m^{opt}\simeq\frac{2b}{\sqrt{3}V}\sqrt{\frac{b}{a}}$	$v_l>v_l^c$ $\tau_1^{opt}\to\infty$ $\tau_2^{opt}\to 0$ $t_m^{opt}\simeq\frac{b}{v_l}$	$v_l<v_l^c\simeq\frac{V}{2}\sqrt{\frac{3a}{b}}$ $\tau_1^{opt}\to 0$ $\tau_2^{opt}\simeq\frac{a}{V}\sqrt{\frac{b}{3a}}$ $t_m^{opt}\simeq\frac{2b}{V}\sqrt{\frac{b}{3a}}$
2D	always intermittence $\tau_1^{opt}=\sqrt{\frac{\tau_2^{opt}}{2k}}\simeq\sqrt{\frac{a}{2Vk}}\left(\ln\left(\frac{b}{a}\right)-\frac{1}{2}\right)^{\frac{1}{4}}$ $\tau_2^{opt}\simeq\frac{a}{V}\sqrt{\ln\left(\frac{b}{a}\right)-\frac{1}{2}}$ $t_m^{opt}\simeq\frac{b^2}{aV}\left(\sqrt{2}\left(\ln\left(\frac{b}{a}\right)\right)^{\frac{1}{4}}+\sqrt{\frac{V}{ak}}\right)^2$	$b<\frac{D}{V}$ $\tau_1^{opt}\to\infty$ $\tau_2^{opt}\to 0$ $t_m^{opt}\simeq\frac{b^2}{2D}\ln\left(\frac{b}{a}\right)$	$b\gg\frac{D}{V}\gg a$ $\tau_1^{opt}\simeq\frac{b^2}{D}\frac{4\ln w-5+c}{w^2(4\ln w-7+c)}$ $\tau_2^{opt}\simeq\frac{b}{V}\frac{\sqrt{4\ln w-5+c}}{w}$ For t_m^{opt}, c and w, see IV B 2	$b\gg a\gg\frac{D}{V}$ $\tau_1^{opt}\simeq\frac{D}{2V^2}\frac{\left(\ln\left(\frac{b}{a}\right)\right)^2}{2\ln\left(\frac{b}{a}\right)-1}$ $\tau_2^{opt}\simeq\frac{a}{V}\sqrt{\ln\left(\frac{b}{a}\right)-\frac{1}{2}}$ $t_m^{opt}\simeq\frac{2b^2}{aV}\sqrt{\ln\left(\frac{b}{a}\right)}$	$v_l>v_l^c$ $\tau_1^{opt}\to\infty$ $\tau_2^{opt}\to 0$ $t_m^{opt}\simeq\frac{\pi b^2}{2av_l}$	$v_l<v_l^c\simeq\frac{\pi V}{4}\left(\ln\left(\frac{b}{a}\right)\right)^{-\frac{1}{2}}$ $\tau_1^{opt}\to 0$ $\tau_2^{opt}\simeq\frac{a}{V}\sqrt{\ln\left(\frac{b}{a}\right)-\frac{1}{2}}$ $t_m^{opt}\simeq\frac{2b^2}{aV}\sqrt{\ln\left(\frac{b}{a}\right)}$
3D	always intermittence $\tau_1^{opt}=\sqrt{\frac{\tau_2^{opt}}{2k}}\simeq\left(\frac{3}{10}\right)^{\frac{1}{4}}\sqrt{\frac{a}{Vk}}$ $\tau_2^{opt}\simeq 1.1\frac{a}{V}$ $t_m^{opt}\simeq\frac{b^3}{\sqrt{5}ka^3}\left(\sqrt{\frac{ak}{V}}24^{\frac{1}{4}}+5^{\frac{1}{4}}\right)^2$	$a\lesssim 6\frac{D}{V}$ $\tau_1^{opt}\to\infty$ $\tau_2^{opt}\to 0$ $t_m^{opt}\simeq\frac{b^3}{3Da}$		$b\gg a\gtrsim 6\frac{D}{V}$ $\tau_1^{opt}\simeq\frac{6D}{V^2}$ $\tau_2^{opt}\simeq 1.1\frac{a}{V}$ $t_m^{opt}\simeq 2.18\frac{b^3}{Va^2}$	$v_l>v_l^c$ $\tau_1^{opt}\to\infty$ $\tau_2^{opt}\to 0$ $t_m^{opt}\simeq\frac{4b^3}{3a^2v_l}$	$v_l<v_l^c\simeq 0.6V$ $\tau_1^{opt}\to 0$ $\tau_2^{opt}\simeq 1.1\frac{a}{V}$ $t_m^{opt}\simeq 2.18\frac{b^3}{Va^2}$

Table II: Recapitulation of main results : strategies minimizing the mean first passage time on the target. In each cell, validity of the regime, optimal τ_1, optimal τ_2, minimal t_m (t_m with $\tau_i=\tau_i^{opt}$). Red highlight the value of τ_2^{opt} independent from the description of the slow detection phase 1. Results are given in the limit $b\gg a$.

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VII. APPENDIX

A. Diffusive mode in dimension 1

1. Exact results (cf. section III B 2)

$$t_m = \frac{1}{3}\frac{(\tau_1+\tau_2)}{\beta^2 b}\frac{Num}{Den} \tag{158}$$

With :

$$Num = \alpha_1+\alpha_2+\alpha_3+\alpha_4+\alpha_5+\alpha_6+\alpha_7 \tag{159}$$

$$Den = \gamma_1+\gamma_2+\gamma_3+\gamma_4 \tag{160}$$

$$\alpha_1 = {L_2}^3\left(\left(3{L_2}^2\left(L_1^2-L_2^2\right)+2h^2\beta\right)h\sqrt{\beta}S+3L_1L_2\left({L_2}^4-2h^2\beta\right)C\right) \tag{161}$$

$$\alpha_2 = -L_1hL_2^5\left(2\beta+3L_2^2\right)RC \tag{162}$$

$$\alpha_3 = L_1\left(2h^4\beta^2-3L_2^8\right)BC \tag{163}$$

$$\alpha_4 = h^2\sqrt{\beta}\left(6L_2^6+h^2\beta\left(\beta+L_1^2\right)\right)RS \tag{164}$$

$$\alpha_5 = \sqrt{\beta}hL_2^3\left(4h^2\beta+3L_2^2\left(L_2^2-L_1^2\right)\right)BS \tag{165}$$

$$\alpha_6 = L_1L_2^3\left(3\left(2h^2L_2\beta+L_2^5\right)B+h\left(3L_2^2\left(\beta+L_2^2\right)+2h^2\beta\right)R\right) \tag{166}$$

$$\alpha_7 = -L_1\left(3L_2^8+2h^4\beta^2\right) \tag{167}$$

$$\gamma_1 = L_2^3L_1R\left(C-1\right) \tag{168}$$

$$\gamma_2 = \sqrt{\beta}h\left(2L_1^2+L_2^2\right)RS \tag{169}$$

$$\gamma_3 = \sqrt{\beta}L_2^3\left(B-1\right)S \tag{170}$$

$$\gamma_4 = 2h\beta L_1\left(BC-1\right) \tag{171}$$

$$B = \cosh\left(\frac{2a}{L_2}\right) \tag{172}$$

$$C = \cosh\left(2h\sqrt{L_1^{-2} + L_2^{-2}}\right) \tag{173}$$

$$R = \sinh\left(\frac{2a}{L_2}\right) \tag{174}$$

$$S = \sinh\left(2h\sqrt{L_1^{-2} + L_2^{-2}}\right) \tag{175}$$

$$\beta = L_1^2 + L_2^2 \tag{176}$$

$$L_1 = \sqrt{D\tau_1} \tag{177}$$

$$L_2 = V\tau_2 \tag{178}$$

$$h = b - a \tag{179}$$

2. Numerical study (cf. section III B 2)

We studied numerically the optimum of the exact t_m expression (158) (Table III). We could distinguish 3 regimes : one with no intermittence, and two with favorable intermittence, but with different scalings. Intermittence is favorable when $b > \frac{D}{V}$. The demarcation line between the two intermittent regimes is $\frac{bD^2}{a^3V^2} = 1$.

3. Details of the optimization of the regime where intermittence is favorable, with $\frac{bD^2}{a^3V^2} \gg 1$ (cf. section III B 4)

We suppose that target density is low : $\frac{a}{b} \ll 1$.

We are interested in the regime where intermittence is favorable. We have both $2(b-a)\sqrt{L_1^{-2} + L_2^{-2}} > 2\frac{b-a}{L_1}$ and $2(b-a)\sqrt{L_1^{-2} + L_2^{-2}} > 2\frac{b-a}{L_2}$. In a regime of intermittence, one diffusion phase does not explore a significant part of the system : $b/L_1 \gg 1$. Alternatively, having a ballistic phase of the size of the system is a waste of time, thus close to the optimum $b/L_2 \gg 1$. Consequently $2(b-a)\sqrt{L_1^{-2} + L_2^{-2}} \gg 1$.

We use the numerical results (Table III) to make assumptions on the dependence of τ_1^{opt} and τ_2^{opt} with the parameters. We define k_1 and k_2 :

$$\tau_1 = (k_1)^{-1}\left(\frac{b^2D}{V^4}\right)^{\frac{1}{3}} \tag{180}$$

	b/a	100	10^3	10^4	10^5	10^6	10^7
a= 0.005	$gain^{th,1}$	0.085	0.39	1.8	8.5	39	180
	$gain$	1	1	2.1	8.7	40	180
	$gain^{th,2}$	0.014	0.046	0.14	0.46	1.4	4.6
	$\tau_1^{th,1}$	0.19	0.89	4.1	19	89	410
	τ_1^{opt}	∞	∞	6.1	21	90	410
	$\tau_1^{th,2}$	2.1	21	210	2100	21000	$2.1.10^5$
	$\tau_2^{th,1}$	0.38	1.8	8.2	38	180	820
	τ_2^{opt}	0	0	8.4	38	180	820
	$\tau_2^{th,2}$	0.029	0.091	0.29	0.91	2.9	9.1
a= 0.5	$gain^{th,1}$	1.8	8.5	39	180	850	4000
	$gain$	2.4	9.4	41	190	850	4000
	$gain^{th,2}$	1.4	4.6	14	46	140	460
	$\tau_1^{th,1}$	4.1	19	89	410	1900	8900
	τ_1^{opt}	3.5	15	78	390	1900	8800
	$\tau_1^{th,2}$	2.1	21	210	2100	21000	$2.1.10^5$
	$\tau_2^{th,1}$	8.2	38	180	820	3800	18000
	τ_2^{opt}	7.6	36	170	810	3800	18000
	$\tau_2^{th,2}$	2.9	9.1	29	91	290	910
a= 50	$gain^{th,1}$	39	180	850	3900	18000	85000
	$gain$	150	470	1500	5500	21000	91000
	$gain^{th,2}$	140	460	1400	4600	14000	46000
	$\tau_1^{th,1}$	89	410	1900	8900	41000	$1.9.10^5$
	τ_1^{opt}	2.2	22	230	2500	21000	$1.4.10^5$
	$\tau_1^{th,2}$	2.1	21	210	2100	21000	$2.1.10^5$
	$\tau_2^{th,1}$	180	820	3800	18000	82000	$3.8.10^5$
	τ_2^{opt}	290	980	3500	15000	72000	$3.6.10^5$
	$\tau_2^{th,2}$	290	910	2900	9100	29000	91000
a= 5000	$gain^{th,1}$	850	3900	18000	85000	$3.9.10^5$	$1.8.10^6$
	$gain$	15000	46000	$1.4.10^5$	$4.6.10^5$	$1.5.10^5$	$4.7.10^6$
	$gain^{th,2}$	14000	46000	$1.4.10^5$	$4.6.10^5$	$1.4.10^6$	$4.6.10^6$
	$\tau_1^{th,1}$	1900	8900	41000	$1.9.10^5$	$8.9.10^5$	$4.1.10^6$
	τ_1^{opt}	2.2	21	210	2100	21000	$2.2.10^5$
	$\tau_1^{th,2}$	2.1	21	210	2100	21000	$2.1.10^5$
	$\tau_2^{th,1}$	3800	1800	82000	$3.8.10^5$	$1.8.10^6$	$8.2.10^6$
	τ_2^{opt}	29000	91000	$2.9.10^5$	$9.2.10^5$	$2.9.10^6$	$9.8.10^6$
	$\tau_2^{th,2}$	29000	91000	$2.9.10^5$	$9.1.10^5$	$2.9.10^6$	$9.1.10^6$

Table III: Diffusive mode in 1 dimension. Optimization of t_m as a function of τ_1 and τ_2 for different sets of parameters ($D = 1$, $V = 1$). For each (a, b), numerical values for the exact analytical function (158) are given with the values expected in the regimes where intermittence is favorable, either with $\frac{bD^2}{a^3V^2} \gg 1$ $(th, 1)$, or with $\frac{bD^2}{a^3V^2} \ll 1$ $(th, 2)$. $gain^{th,1}$ (47), $gain = t_m^{opt}/t_{diff}$, $gain^{2,th}$ (52). $\tau_1^{th,1}$ (44), τ_1^{opt}, $\tau_1^{th,2}$ (49). $\tau_2^{th,1}$ (45), τ_2^{opt}, $\tau_2^{th,2}$ (50). Colors indicate the regime : red when intermittence is not favorable, green in the $\frac{bD^2}{a^3V^2} \gg 1$ regime, blue in the $\frac{bD^2}{a^3V^2} \ll 1$ regime.

$$\tau_2 = (k_2)^{-1} \left(\frac{b^2 D}{V^4} \right)^{\frac{1}{3}} \tag{181}$$

We make a development of t_m for $b \gg a$. We suppose k_1 and k_2 do not depend on b/a :

$$t_m = \frac{1}{3} \frac{D}{V^2} \left(\frac{bV}{D} \right)^{\frac{4}{3}} \frac{k_1 + k_2}{k_1 k_2} \left(k_2^2 + 3\sqrt{k_1} \right) \tag{182}$$

We checked that this expression gives a good approximation of t_m in this regime, in

particular around the optimum (Fig.4, in section III B 4).

Derivatives of (43) as a function of k_1 and k_2 must be equal to 0 at the optimum. It leads to :

$$-3k_1^{\frac{3}{2}} + 3k_2^3 + 3\sqrt{k_1}k_2 = 0 \tag{183}$$

$$3k_1^{\frac{3}{2}} - 2k_2^3 - k_1k_2^2 = 0 \tag{184}$$

On four pairs of solutions, only one is strictly positive :

$$\tau_1^{opt} = \frac{1}{2}\sqrt[3]{\frac{2b^2D}{9V^4}} \tag{185}$$

$$\tau_2^{opt} = \sqrt[3]{\frac{2b^2D}{9V^4}} \tag{186}$$

4. *Details of the optimization of the universal intermittent regime* $\frac{bD^2}{a^3V^2} \ll 1$ *(cf. section III B 5)*

We start from the exact expression of t_m (158). We have to make assumption on the dependency of τ_2^{opt} with b and a. We define f by $\tau_2 = \frac{1}{f}\frac{a}{V}\sqrt{\frac{b}{3a}}$, and we suppose that f is independent from a/b. We make a development of $a/b \to 0$. The first two terms give :

$$t_m \simeq \frac{b}{a}\left(\sqrt{\frac{ab}{3}}\frac{1}{Vf} + \tau_1\right)\frac{a + af^2 + \sqrt{D\tau_1}f^2}{a + \sqrt{D\tau_1}} \tag{187}$$

This expression gives a very good approximation of t_m in the $bD^2/(a^3v^2) \ll 1$ regime, especially close to the optimum (Fig.5, in section III B 5).

We then minimize t_m (187) as a function of f and τ_1. We introduce w defined as :

$$w = \frac{aV}{D}\sqrt{\frac{a}{b}} \tag{188}$$

We make an assumption on the dependency of τ_1^{opt} with a/b, inferred via the numerical results :

$$s = \frac{1}{\tau_1}\frac{D}{V^2}\frac{b}{a} \tag{189}$$

We write the equation (187) with these quantities. Its derivatives with f and s should equal zero at the optimum. It leads to :

$$-\sqrt{3}s^{3/2}w^2 + \sqrt{3}s^{3/2}w^2f^2 + \sqrt{3}s\,wf^2 + 6\sqrt{s}wf^3 + 6\,f^3 = 0 \tag{190}$$

$$6\,s^{3/2}w^2f^3 + 6\,s^{3/2}f\,w^2 - w^2s^2\sqrt{3} + 3\,ws\,f + 12\,ws\,f^3 + 6\sqrt{s}f^3 = 0 \tag{191}$$

We take the equation (190) and here we need to make the assumption than : $a \ll b \ll \frac{a^3V^2}{D^2}$. We get :

$$\sqrt{3}s^{3/2}w^2(f^2-1)=0 \tag{192}$$

Consequently $f=1$. We incorporate this result to equation (191):

$$12\,s^{3/2}w^2 - w^2s^2\sqrt{3} + 15ws + 6\,\sqrt{s} = 0 \tag{193}$$

The relevant solution is :

$$s_{sol} = \left(\frac{1}{3}\frac{\sqrt[3]{u}}{w} + \frac{5\,\sqrt{3}+16\,w}{\sqrt[3]{u}} + \frac{4}{\sqrt{3}}\right)^2 \tag{194}$$

With :

$$u = \left(270\,w + 27\,\sqrt{3} + 192\,w^2\sqrt{3} + 9\,\sqrt{55\,\sqrt{3}w + 84\,w^2 + 27}\right)w \tag{195}$$

When $w \to \infty$, $s_{sol} = 48$. As we made the assumption $\frac{bD^2}{a^3V^2} = w^{-2} \ll 1$, difference from the asymptote will be small (Fig.22).

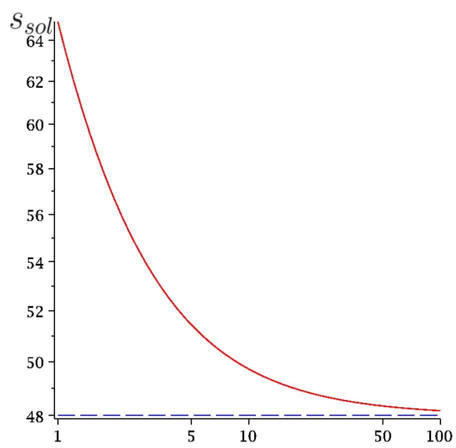

Figure 22: (Color online) Diffusive mode in 1 dimension. s_{sol} (194) (red line) as a function of $\ln(w)$, with the asymptote (blue dotted line)

It leads to :

$$\tau_2^{opt} = \frac{1}{f^{opt}}\frac{a}{V}\sqrt{\frac{b}{3a}} = \frac{a}{V}\sqrt{\frac{b}{3a}} \tag{196}$$

$$\tau_1^{opt} = \frac{Db}{s^{opt}V^2a} = \frac{Db}{48V^2a} \tag{197}$$

It corresponds to numerical results (Table III).

We use equations (41), (48) to calculate the gain.:

$$t_m^{opt} \simeq \frac{2a}{V\sqrt{3}} \left(\frac{b}{a}\right)^{3/2} \tag{198}$$

We get :

$$gain \simeq \frac{1}{2\sqrt{3}} \frac{aV}{D} \sqrt{\frac{b}{a}} \tag{199}$$

It is in very good agreement with numerical data (Table III). Gain can be very large if density is low.

B. Ballistic mode in one dimension : exact result (cf. section III C 2)

$$t_m = \frac{\tau_1 + \tau_2}{b} (\gamma_1 + \gamma_2 + \gamma_3) \tag{200}$$

$$\gamma_1 = \frac{h^2 (h + 3L_1)}{3\alpha} \tag{201}$$

$$\gamma_2 = \frac{L_2 (h + L_1)}{\alpha^{3/2} den} \left(g_4(-1)e^{-\frac{2a}{L_2}} - g_4(1)\right) \left(g_3(-1)e^{2\frac{\sqrt{\alpha}a}{L_1 L_2}} + g_3(1)e^{2\frac{\sqrt{\alpha}b}{L_1 L_2}}\right) \tag{202}$$

$$den = g_1(1)e^{-2\frac{a(L_1 - \sqrt{\alpha})}{L_1 L_2}} + g_1(-1)e^{2\frac{\sqrt{\alpha}b}{L_1 L_2}} + g_2(1)e^{-2\frac{aL_1 - \sqrt{\alpha}b}{L_1 L_2}} + g_2(-1)e^{2\frac{\sqrt{\alpha}a}{L_1 L_2}} \tag{203}$$

$$\gamma_3 = -\frac{L_2}{4\alpha^{3/2}} \frac{num_1 num_2}{den_1 den_2} \tag{204}$$

$$num_1 = f_1(1) + f_1(-1)e^{-\frac{2a}{L_2}} + \sigma_1 + \sigma_2 + \sigma_3 + \sigma_4 \tag{205}$$

$$f_1(\epsilon) = 2\left(\alpha g_4(\epsilon)(h + L_1) + L_2^4 (\epsilon L_2 - L_1)\right) \tag{206}$$

$$\sigma_1 = (f_2(-1) + f_4(1,1) + f_3(1))\, e^{\frac{\sqrt{\alpha}2h}{L_1 L_2}} \tag{207}$$

$$\sigma_2 = (f_2(1) + f_4(1,-1) + f_3(-1))\, e^{-\frac{\sqrt{\alpha}2h}{L_1 L_2}} \tag{208}$$

$$\sigma_3 = (f_4(-1,1) + f_5(1) + f_6(1))\, e^{2\frac{-aL_1 + \sqrt{\alpha}h}{L_1 L_2}} \tag{209}$$

$$\sigma_4 = (f_4(-1,-1) + f_5(-1) + f_6(-1))\, e^{-2\frac{aL_1 + \sqrt{\alpha}h}{L_1 L_2}} \tag{210}$$

$$f_2(\epsilon) = \left(\sqrt{\alpha} + \epsilon L_2\right) L_2 (L_1 - L_2)\, g_3(\epsilon) \tag{211}$$

$$f_3(\epsilon) = -L_2^2 L_1 \sqrt{\alpha}\,(h + L_1)\left(\sqrt{\alpha} + \epsilon L_2 + \epsilon L_1\right) \tag{212}$$

$$f_4(\epsilon_1, \epsilon_2) = h\alpha\,(h + L_1)\left((2L_2 + \epsilon_1 L_1)\left(\epsilon_2\sqrt{\alpha} + L_2\right) + L_1^2\right) \tag{213}$$

$$f_5(\epsilon) = -\epsilon h\sqrt{\alpha} L_2 (L_1 + L_2)\left(2\left(\epsilon\sqrt{\alpha} + L_2\right) L_2 + L_1^2\right) \tag{214}$$

$$f_6(\epsilon) = L_2^2 L_1 \left(L_2\left(\epsilon\sqrt{\alpha}+L_2\right)(L_1+L_2) - \sqrt{\alpha}\,(h+L_1)\left(\sqrt{\alpha}+\epsilon L_2-\epsilon L_1\right)\right) \tag{215}$$

$$num_2 = \varsigma_1+\varsigma_2 - g_4(1)e^{\frac{2a}{L_2}}\left(f_7(1)+f_8(1)\right) - g_4(-1)e^{-\frac{2a}{L_2}}\left(f_7(-1)+f_8(-1)\right) \tag{216}$$

$$\varsigma_1 = 2\sqrt{\alpha}\left(\left(L_2^2-h^2\right)\alpha - L_1^3 h\right)\left(e^{2\,\frac{\sqrt{\alpha}a}{L_1L_2}}+e^{2\,\frac{\sqrt{\alpha}b}{L_1L_2}}\right) \tag{217}$$

$$\varsigma_2 = 2L_2\left(h\,(h+L_1)\,\alpha - L_2^4\right)\left(e^{2\,\frac{\sqrt{\alpha}a}{L_1L_2}}-e^{2\,\frac{\sqrt{\alpha}b}{L_1L_2}}\right) \tag{218}$$

$$f_7(\epsilon) = (\alpha+(L_1+\epsilon L_2)\,h)\sqrt{\alpha}\left(e^{2\,\frac{\sqrt{\alpha}a}{L_1L_2}}+e^{2\,\frac{\sqrt{\alpha}b}{L_1L_2}}\right) \tag{219}$$

$$f_8(\epsilon) = \left(\epsilon h\alpha + L_2^3+\epsilon L_1^3\right)\left(-e^{2\,\frac{\sqrt{\alpha}a}{L_1L_2}}+e^{2\,\frac{\sqrt{\alpha}b}{L_1L_2}}\right) \tag{220}$$

$$den_1 = \sqrt{\alpha}\,(\xi_1+\xi_2+\xi_3+\xi_4+\xi_5+\xi_6+\xi_7) \tag{221}$$

$$\xi_1 = 2L_1\,(h+L_1)\,\alpha \tag{222}$$

$$\xi_2 = L_2\sqrt{\alpha}\left(\left(\alpha+L_2^2\right)\sinh\left(\frac{2h\sqrt{\alpha}}{L_1L_2}\right)+2L_2\sqrt{\alpha}\cosh\left(\frac{2h\sqrt{\alpha}}{L_1L_2}\right)\right) \tag{223}$$

$$\xi_3 = L_1L_2\left(\alpha\sinh\left(\frac{2a}{L_2}\right)-2L_1L_2\cosh\left(\frac{2a}{L_2}\right)\right) \tag{224}$$

$$\xi_4 = -L_2\sqrt{\alpha}\left(\alpha+2L_1h+L_2^2\right)\cosh\left(\frac{2a}{L_2}\right)\sinh\left(\frac{2h\sqrt{\alpha}}{L_1L_2}\right) \tag{225}$$

$$\xi_5 = -2\left(L_1\,(h+L_1)\,\alpha+L_2^4\right)\cosh\left(\frac{2a}{L_2}\right)\cosh\left(\frac{2h\sqrt{\alpha}}{L_1L_2}\right) \tag{226}$$

$$\xi_6 = -L_2\alpha\,(2h+L_1)\sinh\left(\frac{2a}{L_2}\right)\cosh\left(\frac{2h\sqrt{\alpha}}{L_1L_2}\right) \tag{227}$$

$$\xi_7 = -\sqrt{\alpha}\left((2h+L_1)\,\alpha+L_1^3\right)\sinh\left(\frac{2a}{L_2}\right)\sinh\left(\frac{2h\sqrt{\alpha}}{L_1L_2}\right) \tag{228}$$

$$den_2 = g_1(1)e^{-2\,\frac{a\left(L_1-\sqrt{\alpha}\right)}{L_1L_2}}+g_1(-1)e^{2\,\frac{\sqrt{\alpha}b}{L_1L_2}}+g_2(1)e^{-2\frac{aL_1-\sqrt{\alpha}b}{L_1L_2}}+g_2(-1)e^{2\,\frac{\sqrt{\alpha}a}{L_1L_2}} \tag{229}$$

$$g_1(\epsilon) = L_2\,(L_1+L_2)\left(\sqrt{\alpha}-\epsilon L_2\right) \tag{230}$$

$$g_2(\epsilon) = \sqrt{\alpha}\,(2h+L_1)\left(-\epsilon\sqrt{\alpha}-L_2+\epsilon L_1\right)+\epsilon\alpha^{3/2}+L_2^3-\epsilon L_1^3 \tag{231}$$

$$g_3(\epsilon) = h\sqrt{\alpha}\left(-\epsilon\sqrt{\alpha}-L_2\right)+\epsilon 2\,L_2^2L_1 \tag{232}$$

$$g_4(\epsilon) = \left((\epsilon L_2-L_1)\,h+L_2^2\right) \tag{233}$$

$$h = b-a \tag{234}$$

$$\alpha = L_1^2+L_2^2 \tag{235}$$

$$L_1 = v_l\tau_1 \tag{236}$$

$$L_2 = V\tau_2 \tag{237}$$

This result have been checked by numerical simulations and by comparison with known limits.

C. Static mode in 3 dimensions : more comparisons between the analytical expressions and the simulations (cf. section V A 3)

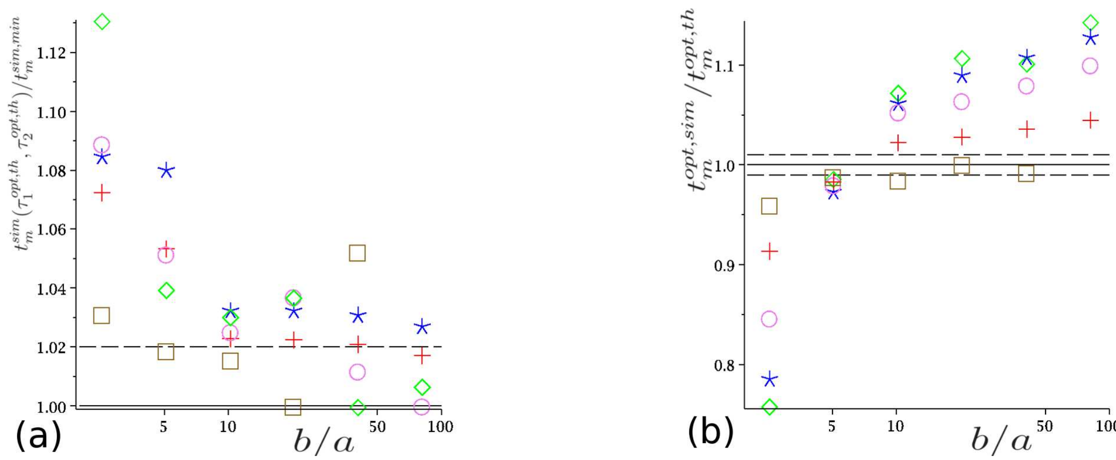

Figure 23: (Color online) Static mode in 3 dimensions. Study of the minimum : its location in the τ_1, τ_2 space (a), and its value (b). *sim* means values obtained through numerical simulations, *th* means analytical values. Value expected if there was a prefect agreement between theory and simulations (black line), and values taking into account the simulations noise (dotted black lines) (we performed 10 000 walks for each point). $a = 0.01$ (brown squares), $a = 0.1$ (red crosses), $a = 1$ (purple circles), $a = 10$ (blue stars), $a = 100$ (green diamonds). $V = 1$, $k = 1$.

The numerical study of the minimum mean search time (Fig.23) shows that the analytical values gives the good position of the minimum in τ_1 and τ_2 as soon as b/a is not too small. However, the value of the minimum is underestimated by about 10%.

D. Diffusive mode in 3 dimensions

1. *Full analytical expression of t_m (cf. section V B 2)*

$$t_m = \frac{1}{b^3\alpha^4 dpD}\left(X + Y + Z\right) \tag{238}$$

with :

$$X = \frac{\left(\tau_1^{-1} + \alpha^2 dp\right)\left(\frac{\alpha^2\left(b^3-a^3\right)}{a} - 3\,S\right)\left(1/3\,\frac{\left(b^3-a^3\right)\left(\alpha^2 dp - \tau_2^{-1}\right)}{a} + \frac{\tau_2^{-1}\left(\alpha\,aR+1\right)}{\alpha^2} + \frac{\alpha\,dp\left(-1+TT\right)}{{\alpha_2}^2}\right)}{\tau_1\left(\left(\tau_1^{-1} + \alpha^2 dp\right)\tau_2^{-1}\,R\alpha + \frac{\left(-\alpha^2 dp + \tau_2^{-1}\right)\tau_1^{-1}}{a} + \frac{TT\,\alpha^2 dp\left(\tau_1^{-1}+\tau_2^{-1}\right)}{a}\right)} \tag{239}$$

$$Y = 3\frac{\tau_1^{-1}\,aS}{\alpha^2} \tag{240}$$

$$Z = -2/30\,\frac{\left(-b+a\right)^3\alpha^2\left(a^3+3\,ba^2+6\,b^2a+5\,b^3\right)\left(\tau_1^{-1}+\alpha^2 dp\right)}{a} \tag{241}$$

$$\alpha = \sqrt{(\tau_1 D)^{-1} + (\tau_2 D_2)^{-1}} \tag{242}$$

$$D_2 = \frac{1}{3}V^2\tau_2 \tag{243}$$

$$dp = \frac{DD_2}{D - D_2} \tag{244}$$

$$\alpha_2 = (\tau_2 D_2)^{-1} \tag{245}$$

$$R = \frac{\alpha\,b\tanh\left(\alpha\ (b-a)\right) - 1}{\alpha\,b - \tanh\left(\alpha\ (b-a)\right)} \tag{246}$$

$$S = \frac{\left(\alpha^2 ba - 1\right)\tanh\left(\alpha\ (b-a)\right) + \alpha\ (b-a)}{\alpha\,b - \tanh\left(\alpha\ (b-a)\right)} \tag{247}$$

$$TT = \frac{\alpha_2\,a}{\tanh\left(\alpha_2\,a\right)} \tag{248}$$

2. Dependence of t_m with τ_1

The mean detection time is very weakly dependent on τ_1 as long as $\tau_1 < 6D/v^2$ (Fig.24).

3. t_m in the regime of diffusion alone (cf. section V B 4)

We take a diffusive random walk starting from $r = r_0$ in a sphere with reflexive boundaries at $r = b$ and absorbing boundaries at $r = a$, we get the following equation for $t(r_0)$ the mean time of absorption :

$$D_{eff}\frac{1}{r_0^2}\left(\frac{d}{dr_0}\left(r_0^2\frac{dt(r_0)}{dr_0}\right)\right) = -1 \tag{249}$$

With the boundary conditions, the solution is :

$$t(r_0) = \frac{1}{6D_{eff}}\left(\frac{2b^3}{a} + a^2 - r_0^2 - \frac{2b^3}{r_0}\right) \tag{250}$$

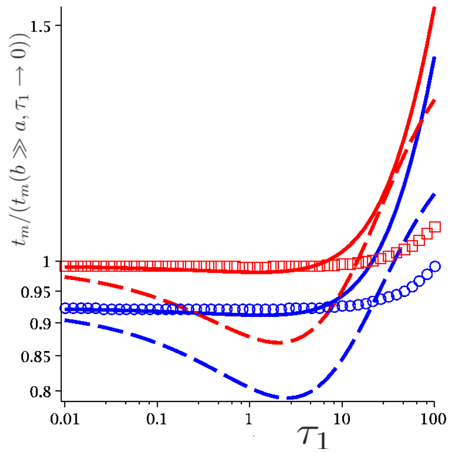

Figure 24: (Color online) Diffusive mode in 3 dimension. t_m from (238), $t_m(b \gg a, \tau_1 \to 0)$ from (144). $\tau_2 = \tau_2^{opt,th}$ (145), $D = 1$, $V = 1$, $a = 10$ (dotted lines), $a = 100$ (lines), $a = 1000$ (symbols), $b/a = 10$ (blue,circles), $b/a = 100$ (red, squares).

Than we average on r_0, as the searcher can start from any point of the sphere with the same probability :

$$t_{diff} = \frac{1}{15Dab^3}\left(5b^3a^3 + 5b^6 - 9b^5a - a^6\right) \tag{251}$$

In the limit $b/a \gg 1$:

$$t_{diff} = \frac{b^3}{3Da} \tag{252}$$

4. Criterion for intermittence : additional figure (cf. section V B 5)

The figure 25 shows the dependence of t_m^{opt} with a.

E. Ballistic mode in 3 dimensions

1. without intermittence (cf. section V C 2)

In the regime without intermittence, τ_1 is not necessarily 0. We calculate t_m in two limits : τ_1 small or τ_1 large.

a. Limit $\tau_2 \to 0$, $v_l\tau_1 \le a$

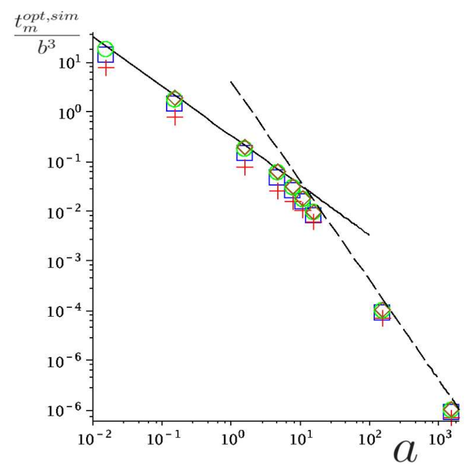

Figure 25: (Color online) Diffusive mode in 3 dimension. Simulations : $b/a = 2.5$ (red crosses), $b/a = 5$ (blue squares), $b/a = 10$ (green circles), $b/a = 20$ (brown diamonds). Analytical expressions in the low target density approximation ($b/a \gg 1$) : $\tau_1 = 0$ (144) (with $\tau_2 = \tau_2^{opt,th}$ (145)) (dotted line), diffusion alone (150) (continuous line). $V = 1$, $D = 1$

In the limit $v_l\tau_1 \leq a$, we can consider phase 1 as diffusive, with :

$$D = \frac{1}{3}v_l^2\tau_1 \tag{253}$$

We use the approached expression of t_m obtained in the diffusive mode (150) with this effective diffusive coefficient.

$$t_m = \frac{1}{5v_l^2\tau_1 ab^3}\left(5b^3a^3 + 5b^6 - 9b^5a - a^6\right) \tag{254}$$

And in the limit $b \gg a$:

$$t_m = \frac{b^3}{v_l^2\tau_1 a} \tag{255}$$

b. limit $\tau_2 \to 0$, $\tau_1 \to \infty$

We name V_{ol} the volume of the sphere. $g(t)$ is the volume explored by the searcher after a time t. The volume explored during dt is $\pi v_l a^2 dt$. If we consider that the probability to encounter a unexplored space is uniform, which is wrong at short times but close to the reality at long times, the average of first explored volume at time t during dt is $\frac{V_{ol}-g(t)}{V_{ol}}\pi v_l a^2 dt$. Then in this hypothesis, $g(t)$ is solution of :

$$g(t) = \int_0^t \frac{V_{ol} - g(u)}{V_{ol}}\pi v_l a^2 du \tag{256}$$

This equation can be simplified taking a renormalized time r as $r = \frac{\pi v_l a^2}{V_{ol}} t$, and $f = g/V_{ol}$:

$$f(r) = \int_0^r (1 - f(w))dw \tag{257}$$

Then, as $f(0) = 0$ (nothing has been explored at time 0), $f(r) = 1 - e^{-r}$. The probability to encounter the target at time t during dt (and not before) is the newly explored volume at time t divided by the whole volume V_{ol} if we make the mean-field approximation. Then the probability $p(r)$ than the target is not yet found at time r is solution of :

$$\frac{dp}{dr} = -(1 - f(u)) \tag{258}$$

As $p(0) = 1$, the result is $p(r) = e^{-r}$. Then the mean detection time of the target is 1 is renormalized time, is to say in real time :

$$t_{bal} = \frac{4b^3}{3a^2 v_l} \tag{259}$$

c. *Numerical study*

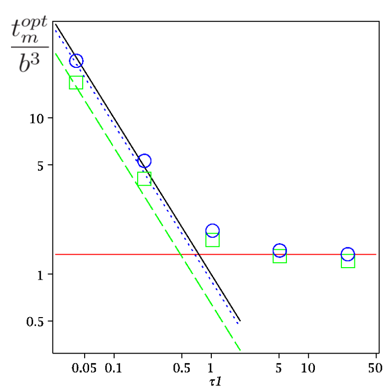

Figure 26: (Color online) Ballistic mode in 3 dimensions. Regime without intermittence ($\tau_2 = 0$). $\ln(t_m/b^3)$ as a function of $\ln(\tau_1)$, simulations for $b = 5$ (green squares) and $b = 20$ (blue circles). Ballistic limit ($\tau_1 \to \infty$) (no intermittence) (152) (red horizontal line), Diffusive limit ($v\tau_1 < a$) (254) with $b = 5$ (green dotted line), $b = 20$ (blue small dots), $b \gg a$ limit (255) (black line). $a = 1$, $v_l = 1$.

These expressions give a very good approximation of the values obtained through simulations (Fig.26, Fig.21). In the regime without intermittence, t_m is minimized for $\tau_1 \to \infty$.

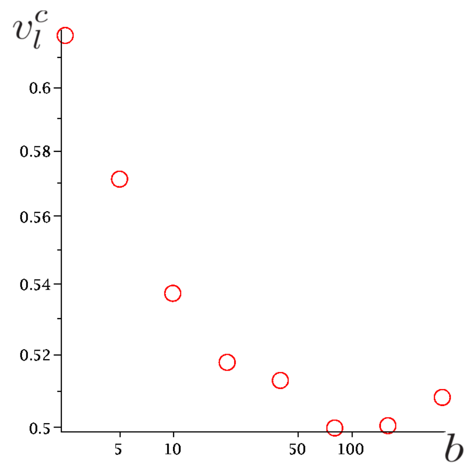

Figure 27: (Color online) Ballistic mode in 3 dimension. v_l^c as a function of $\ln(b)$, through simulations. $a = 1$, $V = 1$.

2. Numerical v_l^c (cf. section V C 4)

In simulations Fig.27, when b is small v_l^c decreases, but stabilizes for larger b, which is coherent with the fact that this value is obtained through a development in b. The value of v_l for large b is different (even if close) to the expected value. The main explanation of this discrepancy is that in the intermittence regime, the approached value of t_m is about 20% away from the value obtained through simulations.